2.2.8. Prairie Vole (voles)

Order *Rodentia* Family *Muridae* (subfamily *Arvicolinae*). New world voles are small, herbivorous rodents that reside in all areas of the United States where good grass cover exists. Their presence is characterized by narrow runways through matted grasses. *Microtus* species are adapted to underground, terrestrial, and sometimes semiamphibious habitats (Johnson and Johnson, 1982). They are active by day and night and feed mainly on shoots, grasses, and bark (Johnson and Johnson, 1982). Voles are prey for snakes, raptors, and mammalian predators such as short-tailed shrews, badgers, raccoons, coyotes, and foxes (Eadie, 1952; Johnson and Johnson, 1982; Martin, 1956).

Selected species

The prairie vole (*Microtus ochrogaster*) represents the ground-burrowing members of this group. This vole is found in the north and central plains of the United States and in southern Canada, usually in dry places such as prairies and along fencerows and railroads. Its range has expanded eastward to West Virginia as a result of clear-cutting of forests (Jones et al., 1983). Voles are active by day or night (Johnson and Johnson, 1982). Although prairie and meadow voles usually occupy different habitats, where they coexist their population densities tend to be negatively correlated (Klatt, 1985; Krebs, 1977).

***Body size*. The prairie vole measures from 8.9 to 13 cm in length and has a 3.0- to 4.1-cm tail (Burt and Grossenheider, 1980). After reaching sexual maturity, voles continue to grow for several months (Johnson and Johnson, 1982). Adults weigh from 30 to 45 g (see table). Prairie voles maintain a relatively constant proportion of their body weight as fat (15 to 16 percent on a dry-weight basis) throughout the year (Fleharty et al., 1973).**

***Habitat*. The prairie vole inhabits a wide variety of prairie plant communities and moisture regimes, including riparian, short-grass, or tall-grass communities (Kaufman and Fleharty, 1974). Prairie voles prefer areas of dense vegetation, such as grass, alfalfa, or clover (Carroll and Getz, 1976); their presence in a habitat depends on suitable cover for runways (Kaufman and Fleharty, 1974). They will tolerate sparser plant cover than the meadow vole because the prairie vole usually nests in burrows at least 50 mm underground or in grass nests under logs or boards (Klatt and Getz, 1987).**

***Food Habits*. Meadow voles, as other voles, are largely herbivorous, consuming primarily green succulent vegetation but also roots, bark, seeds, fungi, arthropods, and animal matter (Johnson and Johnson, 1982; Lomolino, 1984; Stalling, 1990). Voles have masticatory and digestive systems that allow them to digest fibrous grasses such as cereals (Johnson and Johnson, 1982). Diet varies by season and habitat according to plant availability, although meadow and other voles show a preference for young, tender vegetation (Johnson and Johnson, 1982; Martin, 1956). Voles can damage pastures, grasslands, crops such as hay and grain, and fruit trees (by eating bark and roots) (Johnson and Johnson, 1982).**

***Temperature regulation and molt*.** **Unlike some other mammals, prairie voles do not hibernate or exhibit torpor (Johnson and Johnson, 1982). They overwinter without using their lipid reserves, finding food to meet their metabolic requirements year-round (Fleharty et al., 1973). Prairie voles use burrows, runways, nests, and snow cover to help maintain their body temperature. They also modify when they are active to avoid excessively hot or cold temperatures (Johnson and Johnson, 1982). Voles undergo three molts (juvenile, subadult, and adult), and molting may occur at any time during the year (Jameson, 1947, as cited in Stalling, 1990). The subadult-to-adult molt occurs between 8 and 12 weeks of age (Martin, 1956).**

***Breeding activities and social organization*.** **Prairie voles are monogamous; a mated pair occupies the same home range (Thomas and Birney, 1979). Reproduction occurs throughout the year, and gestation lasts approximately 3 wk (Martin, 1956; Keller, 1985; Nadeau, 1985). Both sexes care for the young; paternal activities include runway construction, food caching, grooming, retrieving, and brooding the young (Thomas and Birney, 1979). The young are weaned by about 3 weeks of age (Thomas and Birney, 1979). Reproductive activity peaks from May to October, coinciding with high moisture availability (Martin, 1956; Keller, 1985). Monogamous family units apparently defend territories against other family groups (Ostfeld et al., 1988; Johnson and Johnson, 1982; Thomas and Birney, 1979).**

***Home range and resources*.** **Prairie voles excavate underground nests that are used as nurseries, resting areas, and as shelter from severe weather (Klatt and Getz, 1987). They spend very little time away from this nest (Barbour, 1963). In thick vegetation, prairie voles move about in surface runways, and the number of runways is proportional to population density (Carroll and Getz, 1976). Female home range size decreases with increasing prairie vole density according to the following regression equation (Gaines and Johnson, 1982):**

$Y = -0.23X + 20.16$ where Y= home range length in meters and X= minimum number alive per 0.8 ha grid.

Abramsky and Tracy (1980) found a similar correlation using both sexes according to the equation:

$Y = -0.20X + 27.12$ where Y= home range length in meters and X=number of individuals per hectare.

***Population dynamics*.** **Female prairie voles can reach sexual maturity in about 35 d, males in 42 to 45 d (Gier and Cooksey, 1967, as cited in Stalling, 1990). Martin (1956) found in Kansas that females mature within about 6 wk in the summer, but may require 15 wk or more to mature if born in the fall. Male prairie voles tend to disperse from their natal site; approximately twice as many females as males mature near their birthplace (Boonstra et al., 1987). Populations tend to fluctuate with available moisture (Gier, 1967, as cited in Stalling, 1990). Mortality rates in prairie vole postnestling juveniles and young adults are similar and higher than adult mortality rates; nestlings have the lowest mortality rate (Golley, 1961). Average life expectancy in the field is about 1 yr (Martin, 1956).**

Similar species (from general references)

- **The pine vole (*Microtus pinetorum*) (7 to 11 cm), despite its name, usually inhabits deciduous forest floors, among a thick layer of duff, where it tunnels through loose soil near the surface. It is found in the eastern half of the United States, except Florida; in the south, it inhabits pine forests. In addition to feeding on bark, it burrows for bulbs, tubers, and corms.**

- **See also similar species listed for the meadow vole in this chapter.**

General references

Burt and Grossenheider (1980); Johnson and Johnson (1982); Stalling (1990); Tamarin (1985).

Prairie Vole (*Microtus ochrogaster*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	A B	41.6		ne Colorado	Abramsky & Tracy, 1980	
	A B summer	41.9		ne Colorado	Abramsky & Tracy, 1980	
	A B fall	44.2				
	A B winter	39.0				
	A B spring	41.3				
	A M	31.3 ± 0.35 SE		s Indiana	Myers & Krebs, 1971	
	A F	33.3 ± 0.30 SE				
	neonate B	2.8 ± 0.4 SD		ne Kansas	Martin, 1956	
Metabolic Rate (lO_2/kg-d)	A winter	51.8 ± 8.2 SD		NS/lab	Wunder et al., 1977	
	A summer	41.8 ± 4.8 SD				
Metabolic Rate (kcal/kg-d)	A B basal	177			estimated	1
	A B free-living	399	(190 - 833)		estimated	2
Food Ingestion Rate (g/g-d)	A B at 21°C	0.13 - 0.14		Illinois/lab	Dice, 1922	3
	A B at 28°C	0.09 - 0.10				
Water Ingestion Rate (g/g-d)	A B	0.37		NS/lab	Chew, 1951	4
	A B	0.29 ± 0.02 SE		Kansas/lab	Dupre, 1983	5
	A B	0.21	0.15 to 0.26	Illinois/lab	Dice, 1922	6
	A B	0.14			estimated	7
Inhalation Rate (m^3/d)	A B	0.043			estimated	8
Surface Area (cm^2)	A B	139			estimated	9

Prairie Vole (*Microtus ochrogaster*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
Sporobolus asper		19.5			Kansas/forb and grass field (% volume; stomach contents) (Items less than 2% of volume were combined as "other")	Fleharty & Olson, 1969	
Kochia scoparia		22.5					
Bouteloua gracilis		6.5					
Bromus japonicus		8.5					
Rumex crispus		9.2					
Triticum aestivum		3.4					
Carex sp.		2.0					
other		28.3					
(grasses)		(53.5)					
(forbs)		(46.5)					
Festuca arundinacea	20.5	25.0	10.6	28.9	Missouri/old field (mean number of food items; stomach contents) (Plant parts consumed: leaf, stem, and seeds of *Festuca* and *Bromus*; leaf and stem of *Tridens* and *Setaria faberi*; leaf and seeds of *Dactylis* and *Seteria viridis*; and leaves only of all other plant species)	Cook et al., 1982	
Dactylis glomerata	6.7	1.7	1.1	4.2			
Phleum pratense	8.3	2.0	2.1	5.3			
Tridens flavus	17.1	11.1	1.9	11.0			
Setaria viridis	6.7	6.2	1.7	6.2			
Taraxacum officinale	5.8	4.8	3.9	1.5			
Lamium amplexicaule	3.9	2.9	5.2	3.4			
Bromus tectorum	2.8	4.7	2.5	4.8			
Setaria faberi	5.6	3.9	0.7	21.0			
Capsella bursa-past.	2.7	1.2	0.5	0.6			
Trifolium stolonifera	2.4	0.8	0.5	1.4			
arthropods	0.2	0.3	0.0	0.1			
animal material	0	0.2	0.2	0.0			
other	3.9	1.4	1.5	0.9			

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	A B all yr	0.098 ± 0.012 SE		Illinois/bluegrass	Jike et al., 1988	
	A M all yr A F all yr	0.037 ± 0.0029 SE 0.024 ± 0.0018 SE		Kansas/NS	Swihart & Slade, 1989	
	A M A F	0.011 0.0073		ne Colorado/short-grass prairie	Abramsky & Tracy, 1980	

Prairie Vole (*Microtus ochrogaster*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Population Density (N/ha)	summer winter	25 - 35 12		w Nebraska/xeric prairie	Meserve, 1971	
	spring summer	78 - 118 81 - 104		Illinois/alfalfa field	Carroll & Getz, 1976	
	summer winter spring fall	168 - 234 160 - 197 203 - 247 94 - 123		ne Kansas/grassland	Martin, 1956	
Litter Size		3.18 ± 0.24 SD		ne Kansas/grassland	Martin, 1956	10
		3.4	1 - 7	Kansas/NS	Jameson, 1947	11
		4.25		Illinois/NS	Cole & Batzli, 1978	12
Litters/Year		several		NS/NS	Johnson & Johnson, 1982	
Days Gestation		21 21		ne Kansas/grassland NS/NS	Martin, 1956 Keller, 1985	
Pup Growth Rate (g/d)	days 1 to 10 days 11 to 30 > 30 d until growth stops	0.6 1.0 0.5 (highly variable)		ne Kansas/grassland	Martin, 1956	
Age at Weaning		21 days		NS/lab	Thomas & Birney, 1979	
Age at Sexual Maturity	F M	35 days	 42 to 45 d	NS/NS	Gier & Cooksey, 1967	13
Annual Mortality	B	93 %		ne Colorado/short-grass prairie	Abramsky & Tracy, 1980	
Longevity	B	1 yr	up to 1.8 yr	ne Kansas/grassland	Martin, 1956	

Prairie Vole (*Microtus ochrogaster*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating		May to Oct		NS	Keller, 1985; Martin, 1956	
Parturition		May to Oct		NS	Keller, 1985; Martin, 1956	
Molt		any time		NS	Jameson, 1947	13

1 Estimated using equation 3-43 (Boddington, 1978) and body weights (summer) from Abramsky and Tracy (1980).
2 Estimated using equation 3-48 (Nagy, 1987) and body weights (summer) from Abramsky and Tracy (1980).
3 Estimated from ingestion rate for diet of oats (74 to 78 percent of total weight of diet) and dry grass, assuming 31 to 34 g body weight. Diet was low in water (probably less than 10 percent).
4 Measured water drunk from water bottles; diet consisted of rolled oats with sunflower seeds; temperature 28°C.
5 Measured water drunk; diet of dry food.
6 Temperature 21°C; dry air.
7 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights (summer) from Abramsky and Tracy (1980).
8 Estimated using equation 3-20 (Stahl, 1967) and body weights (summer) from Abramsky and Tracy (1980).
9 Estimated using equation 3-22 (Stahl, 1967) and body weights (summer) from Abramsky and Tracy (1980).
10 Determined from pup count, which may underestimate litter size at birth.
11 Cited in Keller (1985); embryo or pup count.
12 Cited in Keller (1985); embryo or placental scar count.
13 Cited in Stalling (1990).

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2.2.9. Meadow Vole (voles)

Order *Rodentia* Family *Muridae* (subfamily *Arvicolinae*). New world voles are small, herbivorous rodents that reside in all areas of Canada and the United States where there is good grass cover. Their presence is characterized by narrow runways through matted grasses. *Microtus* species are adapted to underground, terrestrial, and sometimes semiamphibious habitats (Johnson and Johnson, 1982). They are active by day and night, feeding mainly on shoots, grasses, and bark. Voles are prey for hawks and owls as well as several mammalian predators such as short-tailed shrews, badgers, and foxes (Johnson and Johnson, 1982; Eadie, 1952).

Selected species

The meadow vole (*Microtus pennsylvanicus*) makes its burrows along surface runways in grasses or other herbaceous vegetation. It is the most widely distributed small grazing herbivore in North America and is found over most of the northern half of the United States. Meadow voles have been used in bioassays to indicate the presence of toxins in their foods (Kendall and Sherwood, 1975, cited in Reich, 1981; Schillinger and Elliot, 1966). Although primarily terrestrial, the meadow vole also is a strong swimmer (Johnson and Johnson, 1982).

***Body size*. The meadow vole measures 8.9 to 13 cm in length (head and body) and has a 3.6- to 6.6-cm tail. They weigh between 20 and 40 g depending on age, sex, and location (see table). Mature males are approximately 20 percent heavier than females (Boonstra and Rodd, 1983). Meadow voles lose weight during the winter, reaching a low around February, then regain weight during spring and summer, reaching a high around August in many populations (see table; Iverson and Turner, 1974).**

***Habitat*. The meadow vole inhabits grassy fields, marshes, and bogs (Getz, 1961a). Compared with the prairie vole, the meadow vole prefers fields with more grass, more cover, and fewer woody plants (Getz, 1985; Zimmerman, 1965). The meadow vole also tends to inhabit moist to wet habitats, whereas the prairie vole is relatively uncommon in sites with standing water (Getz, 1985).**

***Food habits*. Meadow voles consume green succulent vegetation, sedges, seeds, roots, bark, fungi, insects, and animal matter (see table). They are agricultural pests in some areas, feeding on pasture, hay, and grain (Johnson and Johnson, 1982; Burt and Grossenheider, 1980). At high population densities, the meadow vole has been known to girdle trees, which can damage orchards (Byers, 1979, cited in Reich, 1981). In seasonal habitats, meadow voles favor green vegetation when it is available and consume other foods more when green vegetation is less available (Johnson and Johnson, 1982; Riewe, 1973; Getz, 1985). Although Zimmerman (1965) found some evidence of food selection, he found that meadow voles generally ate the most common plants in their habitat. Meadow voles living on prairies consume more seeds and fewer dicots and monocots than voles in a bluegrass habitat (Lindroth and Batzli, 1984). The meadow vole's large cecum allows it to have a high digestive efficiency of 86 to 90 percent (Golley, 1960). Coprophagy (eating of feces) has been observed in this species (Ouellete and Heisinger, 1980).**

***Temperature regulation and molt*.** **In winter, *Microtus* species do not undergo hibernation or torpor; instead, they are active year round (Didow and Hayward, 1969; Johnson and Johnson, 1982). Behaviors that help meadow voles to maintain their body temperature include the use of burrows, runways, nests, and snow cover for insulation. They also can change when they are active; when temperatures exceed 20°C, meadow voles are most active at night (Getz, 1961b; Johnson and Johnson, 1982). In winter, meadow voles increase their brown fat content (a major site of thermoregulatory heat production). Mature individuals average 0.5 percent brown fat in summer, increasing to 1.7 percent in early winter; juveniles average 1.0 percent in the summer, increasing to 2.3 percent in the winter (Didow and Hayward, 1969). Voles undergo three molts: juvenile, postjuvenile, and adult. The timing varies by species (Johnson and Johnson, 1982). Adult *Arvicolinae* also undergo winter and summer molts (Johnson and Johnson, 1982).**

***Breeding activities and social organization*.** **Meadow voles are polygynous (McShea, 1989). Males form a hierarchy in which the most dominant male voles breed (Boonstra and Rodd, 1983). Voles produce litters throughout the breeding season, the number of litters per season increases with decreasing latitude (Johnson and Johnson, 1982).**

***Home range and resources*.** **The area encompassed by a meadow vole's home range depends on season, habitat, population density, and the age and sex of the animal. Summer ranges tend to be larger than winter ranges, and ranges in marshes tend to be larger than ranges in meadows (Getz, 1961c; Reich, 1981). Home range size also declines with increasing population density (Getz, 1961c; Tamarin, 1977a). Female meadow voles defend territories against other females, whereas male home ranges are larger and overlap with home ranges of both sexes (Madison, 1980; Ostfeld et al., 1988; Wolff, 1985). Meadow voles build runways in grasses and vegetation at the ground's surface and use the runways for foraging about 45 percent of the time, depending on weather and other factors (Gauthier and Bider, 1987). The meadow vole exhibits daytime activity where dense cover is available and becomes more crepuscular with less cover (Graham, 1968, cited in Reich, 1981). All *Microtus* species apparently do some burrowing, excavating underground nests that are used as nurseries, resting areas, and as shelter from severe weather (Johnson and Johnson, 1982). Nests are built with the use of dead grass in patches of dense, live grass; widened spaces, called forms, are used off main runways (Ambrose, 1973).**

***Population density*.** **Meadow vole population densities fluctuate widely from season to season and year to year, sometimes crashing to near zero before recovering in a few years to densities of several hundred per hectare (Boonstra and Rodd, 1983; Lindroth and Batzli, 1984; Getz et al., 1987; Myers and Krebs, 1971; Taitt and Krebs, 1985). Krebs and Myers (1974) noted population cycles of 2 to 5 yr, whereas Tamarin (1977b) reported 3- to 4-year population cycles in southeastern Massachusetts. However, Getz et al. (1987) found no indication of multiannual abundance cycles in their three habitat study (i.e., bluegrass, tallgrass prairie, and alfalfa) in east central Illinois. Meadow voles avoid short-tailed shrews (Fulk, 1972), and the vole population density decreases as the number of short-tailed shrews in the area increases (Eadie, 1952).**

***Population dynamics*. Voles reach sexual maturity usually within several weeks after birth, with females maturing before males, but still continue to grow for several months (Johnson and Johnson, 1982). Innes (1978) reported that litter size is independent of latitude or elevation. However, summer litters were, on average, 14 percent larger than litters produced during other seasons, and larger females produced larger litters (Keller and Krebs, 1970). Young from the spring and early summer litters reached adult weight in about 12 wk (Brown, 1973). Mortality rates are highest in postnestling juveniles and young adults and lowest in nestlings (ages 1 to 10 d) (Golley, 1961). Dispersing meadow voles (predominantly young males) tend to weigh less than resident meadow voles (Boonstra et al., 1987; Myers and Krebs, 1971; Boonstra and Rodd, 1983; Brochu et al., 1988).**

Similar species (from general references)

- **The California vole (*Microtus californicus*) is larger than the meadow vole (12 to 14 cm head and body) and is found throughout California and southern Oregon. It inhabits freshwater and saltwater marshy areas, wet meadows, and grassy hillsides from the seashore to the mountains and feeds on green vegetation.**

- **Townsend's vole (*Microtus townsendii*) usually is found near water in moist fields, sedges, tules, and meadows (from tidewater to alpine meadows). Its range is limited to extreme northwestern California, western Oregon and Washington, and southern British Columbia (inhabits several islands off the coast of Washington and British Columbia). It is easily distinguished by its large size (12 to 16 cm) and black-brown color.**

- **The montane vole (*Microtus montanus*) (mountain vole) is slightly larger (10 to 14 cm) than the meadow vole and is found in valleys of the mountainous Great Basin area of the western and northwestern United States.**

- **The long-tailed vole (*Microtus longicaudus*) (tail 5 to 9 cm) is slightly larger (11 to 14 cm) than the meadow vole. It is found in the western United States and Canada to Alaska and lives along streambanks, in mountain meadows, sometimes in dry situations, and in brushy areas during winter. In addition to grasses and bark, it feeds on bulbs. It nests above ground in winter and burrows in summer.**

- **The creeping vole (*Microtus oregoni*) (Oregon vole) (10 to 11 cm) is an inhabitant of western Oregon and Washington and extreme northwest California. Seldom above ground, it spends most of its time burrowing through forest floor duff or grass roots. It lives in forests, brush, and grassy areas.**

- **The sagebrush vole (*Lagurus curtatus*) (9.7 to 11 cm) lives in loose soil and arid conditions and feeds on green vegetation, especially sagebrush. It also burrows around sagebrush; a vole found living in sagebrush is almost certainly this species.**

General references

Burt and Grossenheider (1980); Reich (1981); Johnson and Johnson (1982); Tamarin (1985).

Meadow Vole (*Microtus pennsylvanicus*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	A M summer	40.0 ± 8.3 SE		Quebec, Canada	Brochu et al., 1988	
	A F summer	33.4 ± 8.2 SE				
	A M spring	52.4		Ontario, Canada	Boonstra & Rodd, 1983	
	A F spring	43.5				
	A M & F			Manitoba, Canada	Anderson et al., 1984	
	spring	26.0				
	summer	24.3				
	fall	17.0				
	winter	17.5				
	A M avg. all yr	35.5 ± 0.1 SE		south Indiana	Myers & Krebs, 1971	
	A F avg. all yr	39.0 ± 0.3 SE				
	neonate M & F	2.1	1.6 - 3.0	not specified	Hamilton, 1941	1
	neonate M & F	2.3 ± 0.1 SD			Innes & Millar, 1981	2
Pup Growth Rate (g/d)	birth - 21 days	0.95		south Michigan/old field	Golley, 1961	
	22 - 33 days	0.81				
	34 - 54 days	0.45				
	55 - 103 days	0.19				
Body Fat (g)	summer:			Alberta, Canada	Millar, 1987	
	J F	0.37 ± 0.04 SE				
	A F gestating	1.20 ± 0.15 SE				
	A F lactating	0.60 ± 0.09 SE				
Metabolic Rate (lO_2/kg-d)	basal	60.0		lab	Wiegert, 1961	3
	average daily	82.8 ± 12 SD	43.2 - 146	lab	Morrison, 1948	4
Metabolic Rate (kcal/kg-d)	A M basal	166			estimated	5
	A F basal	175				
	A B avg. daily	395		lab 25-30°C	Pearson, 1947	
	A M free-living	357	(170 - 747)		estimated	6
	A F free-living	485	(231 - 1,020)			

Meadow Vole (*Microtus pennsylvanicus*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Food Ingestion Rate (g/g-d)		0.30 - 0.35		Russia	Ognev, 1950	7
(cal/g-d)	A M short-day A M long-day	370 ± 20 SE 410 ± 10 SE		NS	Dark et al., 1983	8
Water Ingestion Rate (g/g-d)	A B	0.21 ± 0.02 SE		NS	Ernst, 1968	9
	A B	0.14			estimated	10
Inhalation Rate (m^3/d)	A M A F	0.052 0.044			estimated	11
Surface Area (cm^2)	A M A F	161 143			estimated	12

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
dicot shoots	41	60	66	12	Illinois/bluegrass	Lindroth & Batzli, 1984	
monocot shoots	50	26	9	40			
seeds	1	9	1	13	(% volume; stomach contents)		
roots	0	1	12	34			
fungi	6	4	10	0			
insects	2	0	2	1			
dicot shoots	53	65	41	41	Illinois/tallgrass prairie	Lindroth & Batzli, 1984	
monocot shoots	23	29	12	5	(% volume; stomach contents)		
seeds	7	1	16	36			
roots	4	0	6	17			
fungi	12	1	20	0			
insects	1	4	5	1			

Meadow Vole (*Microtus pennsylvanicus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	A M summer A F summer	0.019 ± 0.011 SD 0.0069 ±0.0039 SD		Virginia/old field	Madison, 1980	
	A B summer A B winter	0.014 0.0002		Montana/alluvial bench	Douglass, 1976	
	A M summer A F summer	0.083 ± 0.037 SD 0.037 ± 0.020 SD		Massachusetts/grassy meadow	Ostfeld et al., 1988	
Population Density (N/ha)	A B A B A B		96 - 549 2 - 28 25 - 163	Ontario, Canada/grassland Illinois/bluegrass Indiana/grassland	Boonstra & Rodd, 1983 Lindroth & Batzli, 1984 Myers & Krebs, 1971	
	fall winter spring summer		28 - 51 20 - 51 22 - 53 38 - 64	Michigan/grass-sedge marsh	Getz, 1961a	
Litter Size		3.82 4.46 6.05	1 - 11 1 - 9 1 - 8	Manitoba, Canada/NS Indiana/NS Pennsylvania/NS	Iverson & Turner, 1976 Corthum, 1967 Goin, 1943	13 13 13
Litters/Year		several		NS/NS	Bailey, 1924	14
Days Gestation		21.0 ± 0.2 SD		NS/NS	Kenney et al., 1977	2
Age at Weaning (d)		21		s Michigan/NS	Golley, 1961	
Age at Sexual Maturity	F M		at least 3 wk at least 6-8 wk	NS/NS	Johnson & Johnson, 1982	
Mortality Rates	nestlings juveniles young adults adults old adults	(0-10 g) 50% (11-20 g) 61% (21-30 g) 58% (31-50 g) 53% (>50 g) 100%		south Michigan/old field	Golley, 1961	

Meadow Vole (*Microtus pennsylvanicus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Longevity		2-3 mo		NS	Beer & MacLeod, 1961	9
			< 24 mo	NS	Johnson & Johnson, 1982	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	early April		mid-October	Manitoba, Canada	Mihok, 1984	
		Oct. - Nov.		Michigan (fall-winter peak)	Getz, 1960	15
		April - June		Michigan (spring-summer peak)	Getz, 1960	15
Dispersal		fall/winter		Indiana/grassland	Myers & Krebs, 1971	
		summer (females) winter (males)		Massachusetts/coastal field	Tamarin, 1977b	

1 Cited in Reich (1981) and Johnson and Johnson (1982).
2 Cited in Nadeau (1985).
3 Body weight 35.6 g; temperature not specified; cited in Deavers and Hudson (1981).
4 Temperature 15 to 25°C; weight 26.2 to 32 g.
5 Estimated using equation 3-43 (Boddington, 1978) and body weights from Anderson et al. (1984).
6 Estimated using equation 3-48 (Nagy, 1987) and body weights from Anderson et al. (1984).
7 Cited in Johnson and Johnson (1982).
8 Short-day photoperiod = 10 h of light, 14 of dark; long-day photoperiod = 14 h of light, 10 of dark.
9 Cited in Reich (1981).
10 Estimated using equations 3-17 (Calder and Braun, 1983) and 3-18 and body weights from Anderson et al. (1984).
11 Estimated using equation 3-20 (Stahl, 1967) and body weights from Anderson et al. (1984).
12 Estimated using equation 3-22 (Stahl, 1967) and body weights from Anderson et al. (1984).
13 Cited in Keller (1985).
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2.2.10. Muskrat (water rats and muskrats)

<u>Order *Rodentia* Family *Muridae*</u>. Water rats and muskrats are the most aquatic of this family of rodents, with most of their lives spent in or near bogs, marshes, lakes or streams. These two rodents feed mostly on aquatic vegetation. Only one species exists in each genus (Burt and Grossenheider, 1980).

Selected species

The muskrat (*Ondatra zibethicus*) is indigenous and common throughout most of the United States (except in the extreme southeast, central Texas, and most of California) and Canada (except in the extreme north) (Burt and Grossenheider, 1980). Muskrats feed primarily on aquatic plants. They are prey for hawks, minks, otters, raccoons, owls, red fox, dogs, snapping turtles, and water snakes (Bednarik, 1956; Errington, 1939a; Wilson, 1985), and are more vulnerable to predation during times of drought when low water levels leave their dens or lodges more exposed (Errington, 1939a). Many vertebrates use muskrat homes for shelter or to find food (Kiviat, 1978). The muskrat is one of the most valuable fur animals in North America (Dozier, 1953; Perry, 1982). Including the Newfoundland muskrat, formerly *Ondatra obscurus*, 16 recognized subspecies of *O. zibethicus* exist in North America (Perry, 1982). Of these, *O. z. zibethicus* (eastern United States, southeastern Canada), *O. z. osoyoosensis* (Rocky Mountains, southwestern Canada), and *O. z. rivalicius* (southern Louisiana, coasts of Mississippi, western Alabama, and eastern Texas) are most often studied.

***Body size*. The muskrat measures 25 to 36 cm (head and body) with a 20- to 25- cm tail (Burt and Grossenheider, 1980), and adult weights can range from 0.5 kg to over 2 kg (see Appendix). Willner et al. (1980) reported no sexual dimorphism, whereas Dozier (1950), Parker and Maxwell (1984), and others (see Appendix) reported that males are slightly heavier than females. Muskrats tend to be larger and heavier in northern latitudes (Perry, 1982), although the smallest muskrats are found in Idaho (Reeves and Williams, 1956). Fat levels in adult males increase from spring through fall, and subsequently decrease from winter to spring (Schacher and Pelton, 1975). In nonpregnant females, fat levels decrease from winter through summer; in pregnant females, body fat increases from spring to summer (Schacher and Pelton, 1975).**

***Habitat*. Muskrats inhabit saltwater and brackish marshes and freshwater creeks, streams, lakes, marshes, and ponds (Dozier, 1953; Johnson, 1925; Kiviat, 1978; O'Neil, 1949). Muskrats that live along the banks or shores of waterways generally excavate dens in the banks, whereas muskrats living in ponds with ample plant material construct lodges (Johnson, 1925; Perry, 1982). When available, bank dens seem preferred over constructed lodges (Johnson, 1925).**

***Food habits*. Muskrats are primarily herbivorous, but some populations are more omnivorous (Dozier, 1953; Errington, 1939b). Muskrats usually feed at night, diving to gnaw on aquatic vegetation growing near their houses (Dozier, 1953; Johnson, 1925; Perry, 1982). The roots and basal portions of aquatic plants make up most of the muskrat's diet, although shoots, bulbs, tubers, stems, and leaves also are eaten (Dozier,**

1950, 1953; Willner et al., 1980; Svihla and Svihla, 1931). Marsh grasses and sedges (Svihla and Svihla, 1931) and cattails (Johnson, 1925; Willner et al., 1975) seem to be important muskrat foods; in Maryland, green algae is also important (Willner et al., 1975). Although muskrats forage near their dens or lodges, they show preferences for some plant species (e.g., cattails, bulrushes) over others (Bellrose, 1950). Muskrats are a major consumer of marsh grasses (Kiviat, 1978). They also dig for food on lake and pond bottoms (Bailey, 1937; Dozier, 1953; Hanson et al., 1989). Among the animals that muskrats consume are crayfish, fish, frogs, turtles, and young birds (Errington, 1939b; Johnson, 1925; Willner et al., 1980). Molluscs are an important component of the diet of some populations (Convey et al., 1989; Neves and Odom, 1989; Parmalee, 1989; Willner et al., 1980). Young muskrats feed more on bank vegetation than do adults (Warwick, 1940, cited in Perry, 1982).

***Temperature regulation and molt*. Active year-round (Kiviat, 1978), muskrats usually begin their annual molt in the summer, with fur reaching its minimum density during August (Willner et al., 1980). Muskrats use their dens or lodges to insulate themselves from summer heat and winter cold (O'Neil, 1949; Willner et al., 1980). During extreme cold, muskrats may freeze to death if they are unable to plug their den entrances (Errington, 1939a).**

***Breeding activities and social organization*. Muskrats are solitary or form breeding pairs that remain in a home range exclusive of other pairs (Errington, 1963; Proulx and Gilbert, 1983). They are territorial, particularly during peak reproductive activity, with their houses usually spaced at least 8 m apart (Johnson, 1925; Sather, 1958; Trippensee, 1953). In southern parts of their range, muskrats breed throughout the year, with late fall and early spring peaks (O'Neil, 1949; Svihla and Svihla, 1931; Wilson, 1955). In northern latitudes, breeding occurs only in the spring and summer, with first litters born in late April or early May (Mathiak, 1966; Beer, 1950; Errington, 1937b; Gashwiler, 1950). Errington (1937b) found that postpartum estrus occurs in the muskrat, and suggested that the period between litters is about 30 d. Neonates are almost hairless but by age 2 wk are covered with fur and able to swim (Errington, 1963).**

***Home range and resources*. Muskrats have relatively small home ranges that vary in configuration depending on the aquatic habitat (Perry, 1982; Willner et al., 1980). They build two different types of houses: a main dwelling and a feeding house (feeder) that is smaller than the main house (Dozier, 1953; Johnson, 1925; Sather, 1958). The feeder provides protection from the elements and predators when feeding in prime foraging areas, as well as access to oxygen during frozen conditions. The house provides a dry nest and stable temperatures. Muskrats usually forage within 5 to 10 m of a house (Willner et al., 1980). Using radiotelemetry, MacArthur (1978) found muskrats within 15 m of their primary dwelling 50 percent of the time and only rarely more than 150 m. Mathiak (1966) reported other experiments showing that muskrats remain close to their dwellings.**

In the winter, muskrats build pushups, which are cavities formed in 30 to 46 cm high piles of vegetation pushed up through holes in the ice of a marsh (Perry, 1982). Muskrats use pushups as resting places during frozen conditions to minimize their exposure to cold water (Fuller, 1951). In the summer, muskrats often change the use of their home range in response to water levels; during droughts they will move if the area

around the house dries up, which can lead to intense aggression in the more favorable habitat (Errington, 1939a). Usually only a minor proportion of drought-evicted muskrats can find new homes (Errington, 1939a). In the winter, droughts can result in severe mortality (Errington, 1937a).

***Population density*. Bellrose and Brown (1941, cited in Perry, 1982) concluded that cattail communities support more muskrat houses than other plant types in the Illinois River valley. Cattail communities also support high densities of muskrats in other areas (Errington, 1963; Dozier, 1950). In pond and lake habitats, shoreline length is a more important factor than overall habitat area in determining muskrat density (Glass, 1952, cited in Perry, 1982). Many investigators estimate muskrat densities by counting the number of houses or push-ups and multiplying by a factor ranging from 2.8 (Lay, 1945, cited in Boutin and Birkenholz, 1987) to 5.0 (Dozier et al., 1948), although this method is questionable (Boutin and Birkenholz, 1987).**

***Population dynamics*. The age at first breeding varies but usually occurs during the first spring after birth (Errington, 1963; Perry, 1982). Southern populations produce more litters but with fewer pups in each than do northern populations (Boyce, 1977; Perry, 1982; see table). Muskrats in lower quality habitats have both smaller litter sizes and fewer litters than muskrats in better quality areas (Neal, 1968). They disperse in the spring to establish breeding territories or to move into uninhabited areas (Errington, 1963). Muskrat population cycles of 5, 6, and 10 y have been reported (Butler, 1962; Willner et al., 1980); Perry (1982) summarized several studies that reported cycles ranging from 10 to 14 yr or more. Butler (1962) found that muskrats follow a 10-yr cycle in most parts of Canada.**

Similar species (from general references)

- **The Florida water rat (*Neofiber alleni*) is much smaller (20 to 22 cm) than the muskrat, with a rounded tail (11 to 17 cm) to distinguish it further. The Florida water rat inhabits bogs, marshes, weedy lake borders, and savanna streams, though its range is limited to Florida. It feeds on aquatic plants and crayfish.**

General references

Boutin and Birkenholz (1987); Burt and Grossenheider (1980); Perry (1982); Willner et al. (1980).

Muskrat (*Ondatra zibethicus*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	B M winter B F winter	1,480 1,350	1,400 - 1,520 1,300 - 1,400	New York	Dozier, 1950	
	B M winter B F winter	1,326 ± 45.9 SE 1,221 ± 54.2 SE		e Tennessee	Schacher & Pelton, 1978	
	B M winter B F winter	1,180 1,090	730 - 1,550 770 - 1,450	Nebraska, nc Kansas	Sather, 1958	
	A M spring A F spring	909 837		Idaho	Reeves & Williams, 1956	
	neonate neonate	21.3	16 - 28 20 - 25	Iowa New York	Errington, 1939b Dean, 1957	
	at weaning at weaning	200	112 - 184	Iowa New Brunswick, Canada	Errington, 1939b Parker & Maxwell, 1984	
Pup Growth Rate (g/d)	0 to 30 d	5.4	4.3 - 5.6	Iowa/marsh	Errington, 1939b	
	weaning to 1st fall; M F	7.5 7.1		New Brunswick, Canada/ marsh	Parker & Maxwell, 1980	
Metabolic Rate (lO_2/kg-d)	floating swimming	21 ± 7.9 SE 38		lab (water temperature 25°C)	Fish, 1982	
Metabolic Rate (kcal/kg-d)	floating swimming	101 182		lab (water temperature 25°C)	Fish, 1982	
	A M basal A F basal	71.6			estimated	1
	A M free-living A F free-living	213 216	(90 - 505) (91 - 513)		estimated	2

Muskrat (*Ondatra zibethicus*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Food Ingestion Rate (g/g-d)	greens greens & corn	0.34 0.26		Louisiana, captive (*rivalicius*)	Svihla & Svihla, 1931	3
Water Ingestion Rate (g/g-d)	A M A F	0.97 0.98			estimated	4
Inhalation Rate (m^3/d)	A M A F	0.61 0.57			estimated	5
Surface Area (cm^2)	A M A F	1,221 1,159			estimated	6

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
cattail bulrush burreed waterstarwort pondweed arrowhead corn				25 - 50 10 - 25 5 - 10 2 - 5 2 - 5 2 - 5 2 - 5	ne United States/NS (rough approximation of % diet; stomach contents)	Martin et al., 1951	
cattail rush millet algae grass cord grass seeds other		59 17 8 5 4 4 2 3			Somerset Co., MD/brackish marsh (% of diet; stomach contents)	Willner et al., 1975	

Muskrat (*Ondatra zibethicus*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
green algae 3-square rush switch grass soft rush water willow grass (*Graminae*) other		77 8 8 4 2 1 <1			Montgomery Co., MD/ freshwater (% of diet; stomach contents)	Willner et al., 1975	

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	summer early summer late summer	0.17 ± 0.0078 SD 0.048 ± 0.024 SD 0.11 ± 0.084 SD		Ontario, Canada/marsh Ontario, Canada/bay	Proulx & Gilbert, 1983 Proulx & Gilbert, 1983	
	B M B F	0.17 0.17		Iowa/marsh	Neal, 1968	
Population Density	A B spring A B summer A B fall	9.3 ± 1.3 SE/ha 2.6 ± 0.3 SE/ha 6.3 ± 1.1 SE/ha		ne Iowa/open water riverine	Clay & Clark, 1985	
	B M B M	18.7/ha 2.1/ha		Virginia/fringe marsh Virginia/marsh	Halbrook, 1990	
	B B	28.3/ha	1 - 74	Louisiana/*Scirpus olneyi* marsh	O'Neil, 1949	
	B B summer	23/km river		Pennsylvania/riverine (little vegetation)	Brooks & Dodge, 1986	
	B B summer	48/km river		Massachusetts/wetland, river (sedges)	Brooks & Dodge, 1986	
Litter Size		3.46		Louisiana/marsh	O'Neil, 1949	
		4.65	3 - 6	Virginia/marsh	Halbrook, 1990	
		7.1 ± 0.2 SE		Iowa/riverine	Clay & Clark, 1985	
		7.3	1 - 12	Wisconsin/marsh	Mathiak, 1966	

Muskrat (*Ondatra zibethicus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Litters/Year		1.7 2.1 5 - 6	 < 7 - 8	Idaho/marsh Maine/wildlife refuge - NS Louisiana/NS	Reeves & Williams, 1956 Gashwiler, 1950 O'Neil, 1949	
Days Gestation		29 - 30	> 22 - 23	nw Iowa/marsh Maine/wildlife refuge - NS	Errington, 1937b Gashwiler, 1950	
Age at Weaning	B	28 d	21 - 30 d	Iowa/marsh	Errington, 1939b	
Age at Sexual Maturity		6 mo		Louisiana/marsh	Svihla & Svihla, 1931	
Annual Mortality Rates (%)	adult juvenile juvenile	87 90 67		ne Iowa/riverine Missouri/NS	Clay & Clark, 1985 Schwartz & Schwartz, 1959	 7
Longevity			< 5 yr	Ontario, Canada/marsh	Proulx & Gilbert, 1983	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	year-round	winter spring-summer		southern latitudes northern latitudes	O'Neil, 1949; Svihla & Svihla, 1931 Chamberlain, 1951; Gashwiler, 1950; Reeves & Williams, 1956	
Parturition	late April early May late May	June early July	late August late August mid-August	Iowa Maine Idaho	Errington, 1937b Gashwiler, 1950 Reeves & Williams, 1956	
Dispersal		fall spring		Ontario, Canada Iowa	McDonnell & Gilbert, 1981 Errington, 1963	

Muskrat (*Ondatra zibethicus*)

1 Estimated using equation 3-43 (Boddington, 1978) and body weights from Sather (1958).
2 Estimated using equation 3-46 (Nagy, 1987) and body weights from Sather (1958).
3 Based on wet weight of food; greens included *Panicum hemitomum*, *P. virgatum*, and *Spartina patens*.
4 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Sather (1958).
5 Estimated using equation 3-20 (Stahl, 1967) and body weights from Sather (1958).
6 Estimated using equation 3-22 (Stahl, 1967) and body weights from Sather (1958).
7 Cited in Perry (1982.)

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2.2.11. Eastern Cottontail (rabbits)

<u>Order *Lagomorpha* Family *Leporidae*</u>. Rabbits and hares are medium-sized grazing herbivores found throughout North America. Most species are nocturnal and crepuscular. Many are social, travelling in small groups. Rabbits are prey for large carnivorous birds and mammals. Most species also are important game animals.

Selected species

The eastern cottontail (*Sylvilagus floridanus*) is the most widely distributed of the medium-sized rabbits (Chapman et al., 1982). It is found over most of the eastern half of the United States and southern Canada and has been widely introduced into the western United States (Chapman et al., 1980). North of Mexico, 14 subspecies are recognized (Chapman et al., 1982). The eastern cottontail feeds on green vegetation in summer and bark and twigs in winter. The cottontail is active from early evening to late morning and is preyed on by owls, hawks, and carnivorous mammals (Palmer and Fowler, 1975; Burt and Grossenheider, 1980).

***Body size*. The eastern cottontail measures 35 to 43 cm in length and weighs 0.7 to 1.8 kg (Lord, 1963; see table) with females slightly larger than the males (Nowak and Paradiso, 1983; see table). Cottontail body weight varies seasonally, increasing during spring and summer and declining during winter in some areas; different patterns occur in other areas (Chapman et al., 1982; Pelton and Jenkins, 1970).**

***Habitat*. The eastern cottontail is unique to the genus because of the large variety of habitats that it occupies, including glades and woodlands, deserts, swamps, prairies, hardwood forests, rain forests, and boreal forests (Nowak and Paradiso, 1983). Open grassy areas generally are used for foraging at night, whereas dense, heavy cover typically is used for shelter during the day (Chapman et al., 1982). During winter, cottontails rely more on woody vegetation for adequate cover (Allen, 1984).**

***Food habits*. During the growing season, cottontails eat herbaceous plants (e.g., grasses, clover, timoth, alfalfa). During the winter in areas where herbaceous plants are not available, they consume woody vines, shrubs, and trees (e.g., birch, maple, apple) (Chapman et al., 1982). In Ohio, bluegrass and other grasses made up a large portion of the eastern cottontail's diet, except during snow cover (Chapman et al., 1982). During the winter in Connecticut, the principle diet of eastern and New England cottontails consists of bark and twigs, shrubs and vines, berries, and willow (Dalke and Sime, 1941). In agricultural areas, corn, soybeans, wheat, and other crops may comprise a large portion of their diet (Chapman et al., 1982). Younger rabbits prefer the more succulent weedy forbs that contain more digestible energy and protein (Chapman et al., 1982). Coprophagy (ingestion of feces) has been reported in *S. floridanus* (Kirkpatrick, 1956).**

***Temperature regulation and molt*. Eastern cottontails do not undergo hibernation or torpor; they are active all year, showing peaks of daily activity at dawn and dusk (Chapman et al., 1980). Adults molt gradually over about 9 mo of the year, with two peak molting periods (Spinner, 1940). In Connecticut, the spring peak occurs in May and**

June and the fall peak occurs in September and October (Spinner, 1940). In Texas, spring and fall molts peak in April and October, respectively (Bothma and Teer, 1982).

***Breeding activities and social organization*.** Breeding activity begins later at higher elevations and at higher latitudes (Conaway et al., 1974), by January in Alabama and by late March in southern Wisconsin (Chapman et al., 1980). Several studies have shown that continued harsh winter weather may delay the onset of the breeding season (Hamilton, 1940; Conaway and Wight, 1962; Wight and Conaway, 1961). Breeding seasons are longer in the southern states (Lord, 1960). The onset of breeding varies between different populations and within the same population from year to year (Chapman et al., 1980). Males may fight to establish dominance hierarchies for access to females (Chapman and Ceballos, 1990; Nowak and Paradiso, 1983). Lagomorphs in general are induced ovulators, and cottontails in particular demonstrate a synchronized breeding season, with conception immediately after the birth of a litter (Chapman et al., 1982).

***Home range and resources*.** Cottontails are found in a variety of habitats that contain weedy forbs and perennial grasses; they prefer thick, short, woody perennials that provide escape sites (Chapman and Ceballos, 1990). Cottontails usually do not defend territories; the home ranges of different age and sex groups tend to overlap, especially in fall and winter when they look for areas offering a combination of food and cover (Chapman et al., 1980, 1982). Home ranges are smaller when thick vegetation provides abundant food and larger in habitats with less food (Chapman et al., 1982). Home ranges also are smaller during severe winter weather than at other times (Chapman et al., 1982). During the breeding season, females build elaborate nests within slanting holes in the ground where they give birth to their altricial (helpless) young. These burrows are vulnerable to flooding (Chapman et al., 1982). The size of male home ranges during the breeding season can be more than double that in winter (Nowak and Paradiso, 1983; Trent and Rongstad, 1974).

***Population density*.** Population density depends on the availability of resources (e.g., food, cover) in an area, and tends to cycle over a period of several years (Chapman and Ceballos, 1990). Usual densities range from 1 to 5 animals per hectare, although values as high as 14 per hectare have been reported (Chapman and Ceballos, 1990; Chapman et al., 1982).

***Population dynamics*.** The eastern cottontail exhibits the highest fecundity of the genus; they often produce 25 to 35 young per year (Chapman and Ceballos, 1990). Gestation lasts approximately 1 mo (Chapman et al., 1982). Females may produce five to seven litters per year, and juvenile breeding has been reported (Chapman et al., 1982). The first and last litters of the year are usually the smallest (Chapman et al., 1977). Cottontails have more litters with fewer young each in the southern states (Lord, 1960). Young leave the nest when about age 14 to 16 d, although they may not be fully weaned until a few weeks later (Ecke, 1955). Female cottontails are capable of breeding by age 5 mo, and males as early as 3 mo (Bothma and Teer, 1977). Adult mortality is high, from approximately 65 to 75 percent per year in some places (Eberhardt et al., 1963). Juvenile mortality is even higher, between 85 and 90 percent in the same areas (Eberhardt et al., 1963).

Similar species (from general references)

- **The mountain cottontail (*Sylvilagus nuttallii*) (Nuttall's cottontail) is smaller (30 to 36 cm in length and 0.7 to 1.3 kg) than the eastern cottontail. The only cottontail through most of its range – the western United States – it lives in thickets and sagebrush, around loose rocks, cliffs, and mountains. In the southwest, it lives in forests.**

- **The New England cottontail (*Sylvilagus transitionalis*) is similar in size to the eastern cottontail and inhabits brushy areas, open forests, and mountain terrain in New England, extending down the Appalachians into the southern United States. In recent years, it has disappeared throughout much of the northeastern United States, apparently because of competition with *S. floridanus*.**

- **The desert cottontail (*Sylvilagus audubonii*) (Audubon's cottontail) (30 to 38 cm in length and 0.6 to 1.2 kg) is common in valleys in the arid southwest, although its range extends south to Mexico and north into the Rocky Mountains. It inhabits open plains, foothills, and low valleys and also areas of grass, sagebrush, pinyons and junipers. It is most active from late afternoon throughout the night.**

- **The brush rabbit (*Sylvilagus bachmani*) (28 to 33 cm; 0.6 to 0.8 kg) is usually seen around thick cover and rarely uses a burrow. It feeds on green vegetation, including lawns when in suburban areas. The species is found along the Pacific coast from the Columbia River in the north to the tip of Baja California in the south.**

- **The marsh rabbit (*Sylvilagus palustris*) is similar in size to the eastern cottontail and ranges from southeastern North Carolina to Florida. As the name implies, it inhabits swamps and hummocks, as well as wet bottomlands. Mostly nocturnal, it feeds on marsh vegetation, rhizomes, and bulbs.**

- **The swamp rabbit (*Sylvilagus aquaticus*) is similar in size to the eastern cottontail and is a good swimmer found in swamps, marshes, and wet bottomlands. It ranges primarily in the south, from Texas eastward. It nests beneath logs or in the bases of stumps, rarely using a burrow and may harm crops near swamps.**

- **The pygmy rabbit (*Sylvilagus idahoensis*) is markedly smaller (22 to 28 cm; 0.2 to 0.5 kg) than the eastern cottontail, lacks a conspicuous tail, and is considered by some to be a distinct genus (*Brachylagus*). Its range is limited to several western states, where it inhabits clumps of tall sagebrush. It is mostly nocturnal.**

- **The white-tailed jackrabbit (*Lepus townsendii*), larger (46 to 56 cm; 2.2 to 4.5 kg) than the eastern cottontail, is limited to the northern United States**

west of the Great Lakes, into southern Canada. It inhabits open, grassy, or sagebrush plains and may damage hay crops and small trees.

- **The black-tailed jackrabbit (*Lepus californicus*) (43 to 53 cm; 1.3 to 3.1 kg) is the most common jackrabbit in the grasslands and open areas of the western United States, where it inhabits open prairies and deserts with little vegetation. It is mostly nocturnal.**

- **The snowshoe hare (*Lepus americanus*) (33 to 46 cm; 0.9 to 1.8 kg) inhabits swamps, forests, and thickets in the northern United States and Canada. During summer, it feeds on succulent vegetation and during winter on twigs, buds, and bark. Its home range is about 4 ha, but populations fluctuate widely.**

General references

Allen (1984); Burt and Grossenheider (1980); Chapman et al. (1980, 1982); Lord (1963); Nowak and Paradiso (1983); and Palmer and Fowler (1975).

Eastern Cottontail (*Sylvilagus floridanus*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	A M A F	1,134 ± 122 SD 1,244 ± 165 SD	801 - 1,411 842 - 1,533	w Maryland, West Virginia	Chapman & Morgan, 1973	
	A B winter A B spring A B summer A B fall	1,176 1,286 1,197 1,255	793 - 1,671 898 - 1,630 910 - 1,608 886 - 1,669	Georgia all areas combined	Pelton & Jenkins, 1970	
	A B not breed. A B not breed. A B not breed.	1,229 ± 113 SD 1,313 ± 141 SD 1,132 ± 136 SD	1,093 - 1,461 986 - 1,671 793 - 1,579	Georgia mountain coastal Piedmont	Pelton & Jenkins, 1970	
	A B	1,231 ± 164	700 - 1,800	Illinois	Lord, 1963	
	neonate	42.2	36.0 - 49.0	Alabama	Hill, 1972b	
	age: 10 d 30 d 50 d 101 d 149 d	 58 159 401 822 1,106		Illinois	Lord, 1963	
Growth Rate (g/d)	day 0 - 30 day 11 - 30 day 31 - 50 day 51 - 100 day 101 - 150	3.2 3.7 8.8 11.3 6.4		Illinois	Lord, 1963	
Metabolic Rate (kcal/kg-d)	A B basal	71			estimated	1
	A B free-living	203	(77 - 535)		estimated	2
Food Ingestion Rate (g/g-d)						3
Water Ingestion Rate (g/g-d)	A B	0.097			estimated	4

Eastern Cottontail (*Sylvilagus floridanus*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Inhalation Rate (m^3/d)	A B	0.63			estimated	5
Surface Area (cm^2)	A B	1,254			estimated	6

Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat(measure)	Reference	Note No.
trees shrubs & vines herbs grasses, sedges, rushes crops	13 4 44 26 13	2 2 23 56 17	7 27 34 30 2	39 40 5 6 10	Connecticut (*mallarus*)/ various (% frequence of occurrence; observations of feeding on plants)	Dalke & Sime, 1941 (85% for *mallarus* subspecies, remainder for similar species *S. transitionalis*)	
woody plants forbs grasses	17 19 64	23 30 47	20 46 34	100	Maryland/forest (% frequency of occurrence; stomach contents)	Spencer & Chapman, 1986	
bluegrass orchard grass timothy grass Nodding wild rye Canada goldenrod red clover unidentified	34 4 5 5 - - 52	34 1 12 11 - - 42	25 - 7 8 3 6 51	32 1 1 4 - - 62	Ohio (*mearnsi*)/NS (% frequency of occurrence; scats) (in winter, woody tissues predominated in the unidentified category)	Dusi, 1952	

Eastern Cottontail (*Sylvilagus floridanus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/Habitat	Reference	Note No.
Home Range Size (ha)	A M winter	3.05 ± 0.72 SE		Wisconsin/woodlot	Dixon et al., 1981	
	A F winter	2.99 ± 0.28 SE				
	A M winter	3.2		c Pennsylvania/mixed	Althoff and Storm, 1989	
	A M spring	7.2				
	A M summer	7.8				
	A M fall	3.1				
	A F winter	2.1		c Pennsylvania/mixed	Althoff and Storm, 1989	
	A F spring	2.8				
	A F summer	2.4				
	A F fall	1.5				
	A M spring	2.8		sw Wisconsin/woodlot	Trent & Rongstad, 1974	
	A M					
	early summer	4.0				
	late summer	1.5				
	A F spring	1.7				
	A F summer	0.8				
Population Density (N/ha)	fall	1.1 ± 0.41 SD	0.41 to 2.08	c Michigan/woods, marsh, fields	Eberhardt et al., 1963	
	fall		3.0 - 5.9	Illinois/old field	Lord & Casteel, 1960	
	winter		0.67 - 1.5			
	summer	4.2		sw Wisconsin/farm	Trent & Rongstad, 1974	
	fall	10.1				
	spring	3.7				
Litter Size		3.5 ± 0.042 SE		Alabama/across six habitats	Hill, 1972c	
		5.3		Illinois/NS	Lord, 1963	
		6.0		Missouri/wildlife area	Conaway et al., 1963	
Litters/Year		4.6		w Maryland/NS	Chapman et al., 1977	
			5 - 7	several locations and habitats	Chapman et al., 1980	7
Days Gestation		28	25 - 35	several locations and habitats	Chapman et al., 1982	

Eastern Cottontail (*Sylvilagus floridanus*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/Habitat	Reference	Note No.
Age at Weaning		20 - 25 days		Illinois/NS	Ecke, 1955	
Age at Sexual Maturity	F M		3 - 6 months 3 - 6 months	s Texas/grassland Missouri/NS	Lord, 1961, Negus, 1959b Conaway & Wight, 1963	8
Annual Mortality Rates (%)	B B B B	80 65 ± 7 SD		sw Wisconsin/farm Illinois/sanctuary	Trent & Rongstad, 1974 Lord, 1963	
Longevity	B	1.25		Kentucky/NS	Bruna, 1952	9

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	mid-March year-round	 January - April	mid-September	Connecticut s Texas	Dalke, 1942 Bothma & Teer, 1977	9
Parturition	April	May - July	August	wc New York	Hamilton, 1940	
Molt fall	August September	October Sept. - Oct.	December November	s Texas Connecticut	Bothma & Teer, 1982 Spinner, 1940	
spring	February March	April May - June	July August	s Texas Connecticut	Bothma & Teer, 1982 Spinner, 1940	

1 Estimated using equation 3-43 (Boddington, 1978) and body weights from Lord (1963).
2 Estimated using equation 3-46 (Nagy, 1987) and body weights from Lord (1963).
3 See Chapters 3 and 4 for approaches to estimating food ingestion rates.
4 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Lord (1963).
5 Estimated using equation 3-20 (Stahl, 1967) and body weights from Lord (1963).
6 Estimated using equation 3-22 (Stahl, 1967) and body weights from Lord (1963).
7 Summary of several studies.
8 Cited in Conaway and Wight (1963).
9 Cited in Chapman et al. (1980).
10 Cited in Chapman et al. (1982).

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2.3. REPTILES AND AMPHIBIANS

Table 2-3 summarizes the species of reptiles and amphibians included in this section. For range maps, refer to the general references identified in the individual species profiles. The remainder of this section is organized by species in the order presented in Table 2-3. The availability of information in the published literature varies substantially among species, which is reflected in the profiles. The measures used to describe body length are included in each species profile. Body weight is reported as fresh wet weight (including the shell for turtles), unless otherwise noted.

Unlike birds and mammals for which a single common name usually covers all subspecies, many reptile and amphibian subspecies are recognized by different common names. For example, there are two subspecies of *Rana clamitans*: the green frog and the bronze frog (Section 2.3.7). There are four subspecies of *Terrapene carolina*: eastern box turtle, three-toed box turtle, Florida box turtle, and Gulf Coast box turtle (Section 2.3.3). In this case, other species exist that are also known as box turtles: the ornate and desert box turtles belong to the species *T. ornata*. For species that could be confused with other species unless a subspecies common name is used, we selected the common name of the most widespread subspecies to use in the tables and titles of the species profile. As with the other species in the Handbook, however, the profile covers all subspecies for the selected species that were represented in the literature reviewed.

In these profiles, we use the word hibernation for the period of dormancy that reptiles and amphibians undergo during winter, when they change their metabolism to accommodate the low (often near freezing) temperatures and lack of food (and oxygen). Use of the word for this group is controversial, however, because the word was developed initially to describe mammalian winter dormancy. Some investigators argue that a different word, brumation, should be established to describe the overwintering dormancy and associated metabolic changes for reptiles and amphibians (Hutchison, 1979). Others disagree, because significant physiological changes also occur in reptiles and amphibians during winter dormancy. They argue that, although the physiological changes are different from those in mammals, the word hibernation is a general term that does not specify what

Table 2-3. Reptiles and Amphibians Included in the Handbook

Order	Common name	Scientific name	Section
Chelydridae	snapping turtle	*Chelydra serpentina*	2.3.1
Emydidae	painted turtle	*Chrysemys picta*	2.3.2
	eastern box turtle[a]	*Terrapene carolina carolina*	2.3.3
Colubridae	racer	*Coluber constrictor*	2.3.4
	northern water snake[a]	*Nerodia sipedon sipedon*	2.3.5
Salamandridae	eastern newt	*Notophthalmus viridescens*	2.3.6
Ranidae	green frog[a]	*Rana clamitans clamitans*	2.3.7
	bullfrog	*Rana catesbeiana*	2.3.8

[a]Additional subspecies also are included in the profile.

metabolic changes occur to allow overwintering in a dormant state (Gatten, 1987). We have chosen this latter interpretation for the Handbook.

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2.3.1. Snapping Turtle (snapping turtles)

<u>Order *Testudines*, Family *Chelydridae*</u>. Snapping turtles are among the largest of the freshwater turtles. They are characterized by large heads with powerful hooked jaws. There are only two species of this family in North America (the snapping turtle, including both the common and Florida snapping turtles, and the alligator snapping turtle).

Selected species

The snapping turtle (*Chelydra serpentina*) is primarily aquatic, inhabiting freshwater and brackish environments, although they will travel overland (DeGraaf and Rudis, 1983; Ernst and Barbour, 1972; Smith, 1961). There are two subspecies recognized in North America that are primarily distinguished by range: *C. s. serpentina* (the common snapping turtle, which is the largest subspecies, primarily occupies the United States east of the Rockies, except for the southern portions of Texas and Florida), and *C. s. osceola* (the Florida snapping turtle, found in the Florida peninsula) (Conant and Collins, 1991). In this profile, studies refer to the *serpentina* subspecies unless otherwise noted.

***Body size*. Adult snapping turtles are large, 20 to 37 cm in carapace length, and males attain larger sizes than females (Congdon et al., 1986; Ernst and Barbour, 1972; Galbraith et al., 1988). In a large oligotrophic lake in Ontario Canada, adult males averaged over 10 kg, whereas the females averaged 5.2 kg (Galbraith et al., 1988). In other populations, the difference in size between males and females often is less (Congdon et al., 1986; Galbraith et al., 1988; Hammer, 1969). They reach sexual maturity at approximately 200 mm in carapace length (Mosimann and Bider, 1960). The cool, short activity season in more northern areas results in slower growth rates and longer times to reach sexual maturity (Bury, 1979).**

***Habitat*. In the east, snapping turtles are found in and near permanent ponds, lakes, and marshes. However, in the arid west, the species is primarily found in larger rivers, because these are the only permanent water bodies (Toner, 1960, cited in Graves and Anderson, 1987). They are most often found in turbid waters with a slow current (Graves and Anderson, 1987). They spend most of their time lying on the bottom of deep pools or buried in the mud in shallow water with only their eyes and nostrils exposed. Froese (1978) observed that young snapping turtles show a preference for areas with some obstructions that may provide cover or food.**

***Food habits*. Snapping turtles are omnivorous. In early spring, when limited aquatic vegetation exists in lakes and ponds, they may eat primarily animal matter; however, when aquatic vegetation becomes abundant, they become more herbivorous (Pell, 1941, cited in Graves and Anderson, 1987). Young snapping turtles are primarily carnivorous and prefer smaller streams where aquatic vegetation is less abundant (Lagler, 1943; Pell, 1941, cited in Graves and Anderson, 1987). Snapping turtles consume a wide variety of animal material including insects, crustaceans, clams, snails, earthworms, leeches, tubificid worms, freshwater sponges, fish (adults, fry, and eggs), frogs and toads, salamanders, snakes, small turtles, birds, small mammals, and carrion and plant material including various algae (Alexander, 1943; Graves and Anderson, 1987; Hammer, 1969;**

Punzo, 1975). Budhabatti and Moll (1988) observed no difference between the diets of males and females who fed at the surface, midpelagic, and benthic levels. Bramble (1973) suggested that the pharyngeal mechanism of feeding (i.e., drawing water with food objects into the mouth) prevents snapping turtles from ingesting food above the air-water interface.

***Temperature regulation and daily activities*. Snappers are most active at night. During the day, they occasionally leave the water to bask on shore, but basking is probably restricted by intolerance to high temperatures and by rapid loss of moisture (Ernst and Barbour, 1972). In a study in Ontario, Canada, Obbard and Brooks (1981) found that the turtles were active in the early morning and early evening and basked in the afternoon but were rarely active at night. Active turtles were found in deeper waters than inactive snappers (Obbard and Brooks, 1981). Cloacal temperatures of 18.7 to 32.6°C were reported for snapping turtles captured in the water in Sarasota County, Florida, between May and October (Punzo, 1975).**

***Hibernation.* Snapping turtles usually enter hibernation by late October and emerge sometime between March and May, depending on latitude and temperature. To hibernate, they burrow into the debris or mud bottom of ponds or lakes, settle beneath logs, or retreat into muskrat burrows or lodges. Snapping turtles have been seen moving on or below the ice in midwinter. Large congregations sometimes hibernate together (Budhabatti and Moll, 1988; Ernst and Barbour, 1972).**

***Breeding activities and social organization*. Mating occurs any time turtles are active from spring through fall, depending on latitude (Ernst and Barbour, 1972). Some investigators believe that male snapping turtles are territorial (Kiviat, 1980; Pell, 1941, cited in Galbraith et al., 1987), but Galbraith et al. (1987) doubts that males defend their home ranges against other males. Sperm may remain viable in the female for several years (Smith, 1956). Nesting occurs from late spring to early fall, peaking in June (Ernst and Barbour, 1972). Hammer (1969) observed that larger, older females nested earlier in the season than did smaller, younger ones. Females often move up small streams to lay eggs (Ewert, 1976, cited in Graves and Anderson, 1987). The nest site may be in the soil of banks or in muskrat houses but more commonly is in the open on south-facing slopes and may be several hundred meters from water (DeGraaf and Rudis, 1983). The turtle digs a 4- to 7-in cavity on dry land, preferably in sand, loam, or vegetable debris. The duration of incubation is inversely related to soil temperature (Ernst and Barbour, 1972; Yntema, 1978, cited in Graves and Anderson, 1987). In more northerly populations, hatchlings may overwinter in the nest (DeGraaf and Rudis, 1983).**

***Home range and resources*. Most turtles stay primarily within the same marsh or in one general area from year to year ((Hammer, 1969; Obbard and Brooks, 1981). The summer home range includes a turtle's aquatic foraging areas, but females may need to travel some distance outside of the foraging home range to find a suitable nest site (DeGraaf and Rudis, 1983). Obbard and Brooks (1980) found that females tagged at their nesting site moved an average of 5.5 km (± 1.8 SD) from the nest site afterwards. Lonke and Obbard (1977) observed that 91.9 percent of the turtles in one population returned to the same nesting site a year after having been tagged there. Home ranges overlap both between and within sexes (Obbard and Brooks, 1981). Young snapping turtles use**

different habitats than adults; they tend to remain in small streams until shortly before maturity, when they migrate to habitats preferred by adults (e.g., ponds, marshes, lakes) (Hammer, 1971; Minton, 1972, cited in Graves and Anderson, 1987).

***Population density*. The density of snapping turtles appears to be positively correlated with the productivity of the surface water body (e.g., density in a eutrophic surface water body is higher than in an oligotrophic lake) (Galbraith et al., 1988). Specific habitat characteristics and intraspecific interactions contribute to the variability of observed population densities in snapping turtles (Froese and Burghardt, 1975).**

***Population dynamics*. Females do not begin laying eggs until age 6 to 19 yr depending on latitude and when they reach an appropriate size (approximately 200 mm carapace) (Galbraith et al. 1989; Mosimann and Bider, 1960). Males mature a few years earlier than females (see table). Females may lay one or two clutches per season (Minton, 1972, cited in Graves and Anderson, 1987). Clutch size increases with female body size; Congdon et al. (1987) calculated the relationship between clutch size (CS) and plastron length (PL in mm) for a population in southeastern Michigan:**

$$CS = -21.227 + 0.242\ PL,\ (r^2 = 0.409,\ n = 65).$$

Clutch size has also been positively correlated with latitude (Petokas and Alexander, 1980). Hammer (1969) found that mammalian predators destroyed over 50 percent of the turtle nests in a South Dakota marsh, and in undisturbed nests, hatchling success was less than 20 percent. Petokas and Alexander (1980) observed a 94 percent predation rate of nests under study in northern New York. Adult mortality is low, corresponding with the long lives exhibited by these turtles (see table).

Similar species (from general references)

- **The alligator snapping turtle (*Macroclemys temmincki*) is much larger (16 to 68 kg; 38 to 66 cm carapace) than the common snapping turtle and is one of the largest turtles in the world. Its range is from northern Florida to east-central Texas and north in the Mississippi Valley.**

General references

Conant and Collins (1991); DeGraaf and Rudis (1983); Ernst and Barbour (1972); Graves and Anderson (1987).

Snapping Turtle (*Chelydra serpentina*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (kg)	A M summer A F summer J B summer	10.5 ± 2.85 SD 5.24 ± 0.85 SD 1.15 ± 0.80 SD		Ontario, Canada/large oligotrophic lake	Galbraith et al., 1988	
	A M summer A F summer J B summer	5.52 ± 2.23 SD 5.03 ± 1.12 SD 1.40 ± 0.20 SD		Ontario, Canada/eutrophic pond	Galbraith et al., 1988	
	A M A F J B	4.16 ± 0.28 SE 3.16 ± 0.20 SE 0.80 ± 0.07 SE		Michigan	Congdon et al., 1986	
	at hatching	0.0057		NS	Ernst & Barbour, 1972	
	at hatching	0.0089		NS	Ewert, 1979	
	mm carapace: 118 127 134 167 192 220	 0.33 0.44 0.53 1.03 1.51 2,362		Massachusetts	Graham & Perkins, 1976	
Egg Weight (g)			7 - 15	NS	Ernst & Barbour, 1972	
		11.1		northern New York	Petokas & Alexander, 1980	
		9.6		South Carolina	Congdon et al., 1986	
		9.3	5.7 - 13.8	New Jersey	Hotaling et al., 1985	
Body Length (mm carapace)	age in years 1 2 3 4 5 6	 62 ± 4.5 SD 102 ± 5.8 SD 137 ± 9.4 SD 168 ± 14.2 SD 198 ± 13.7 SD 222 ± 12.9 SD	 54 - 66 83 - 108 124 - 145 146 - 184 177 - 211 204 - 238	Michigan	Gibbons, 1968	

Snapping Turtle (*Chelydra serpentina*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Metabolic Rate (lO_2/kg-d)	7.18 kg, rest 25°C	2.54			Lynn & von Brand, 1945	1
Metabolic Rate (kcal/kg-d)	A F basal A M basal	3.2 3.0			estimated	2
Food Ingestion Rate (g/g-d)	B summer		0.01 - 0.016	New York/captivity	Kiviat, 1980	

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
adults & juveniles: plants animals		 35 - 70 6 - 35			location not specified (% of diet; measure NS)	Smith, 1956	3
adults: fish vegetation clams mud & rocks		 83.7 13.6 0.2 2.5			Tennessee/embayment (% wet volume; gastro-intestinal tract contents)	Meyers-Schoene & Walton, 1990	
adults & juveniles: (plants) algae (animals) crayfish fiddler crab sucker bullhead sunfish unknown fish (miscellaneous)		 (36.5) 12.8 (54.1) 8.9 2.7 3.2 6.3 7.5 12.4 (9.4)			Connecticut/lakes, ponds, streams, swamps (% wet volume; stomach contents)	Alexander, 1943	

Snapping Turtle (*Chelydra serpentina*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Home Range Size (ha)	A M summer	0.7 ± 0.29 SD	0.24 - 1.3	Ontario, Canada/lake	Galbraith et al., 1987	
	A F summer A M summer A B summer	3.79 ± 1.46 SD 3.21 ± 2.67 SD 3.44 ± 2.18 SD	2.5 - 5.19 0.95 - 8.38	Ontario, Canada/lake	Obbard & Brooks, 1981	
	A M A F nonbreed	8.9 7.2		New York/fresh tidal wetland	Kiviat, 1980	
Population Density (N/ha)				Ontario, Canada/		
	A M summer	1.5		oligotrophic lake	Galbraith et al., 1987	
	B B summer	2.3 ± 1.45 SD	1.0 - 4.9	oligotrophic waters	Galbraith et al., 1988	4
	B B summer	60.4	40.3 - 95.0	eutrophic pond	Galbraith et al., 1988	
	B B summer	29.3 ± 27.6 SD	4.4 - 65.9	eutrophic ponds (other studies)	Galbraith et al., 1988	5
	A B summer	59		Tennessee/pond	Froese & Burghardt, 1975	
Clutch Size		49.0	31 - 87	South Dakota/marsh	Hammer, 1969	
		27.9 ± 0.76 SE	12 - 41	se Michigan/NS	Congdon et al., 1987	
		16.6 ± 1.6 SD	14 - 20	Florida/NS	Iverson, 1977	6
Clutches/Year			1 - 2	Indiana/NS	Minton, 1972	7
		> 1		NS/summarizing other studies	Ernst & Barbour, 1972	
Days Incubation		105	90 - 119	Ontario, Canada/lake	Obbard & Brooks, 1981	
			67 - 73	se Wisconsin/NS	Ewert, 1979	
Age at Sexual Maturity (yr)	F nesting	6 - 8		New York/NS	Pell, 1941	8
	F nesting M	9 - 10 4 - 5		Iowa/NS	Christiansen & Burken, 1979	
	F nesting	17 - 19	at least 14 to 15	Ontario, Canada/riverine, mixed forest	Galbraith et al., 1989	

Snapping Turtle (*Chelydra serpentina*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Length at Sexual Maturity	A B	200 mm carapace		Quebec, Canada/NS	Mosimann & Bider, 1960	
	A B	145 mm plastron		Tennessee/NS	White & Murphy, 1973	9
Annual Mortality Rates (%)	A B		3 - 7	NS/NS	Galbraith & Brooks, 1987	10
Longevity (yr)			at least 24	Michigan/marsh	Gibbons, 1987	
			at least 19	South Carolina/river	Gibbons, 1987	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	April early June mid-June	June mid-June	November end of June	depends on latitude New York Florida	Ernst & Barbour, 1972 Kiviat, 1980 Punzo, 1975	
Nesting	May late May early June	June early to mid-June mid-June	September late June end of June	depends on latitude northern New York South Dakota	Ernst & Barbour, 1972 Petokas & Alexander, 1980 Hammer, 1969	
Hatching	August late August	 September	October early October	depends on latitude se Michigan	Ernst & Barbour, 1972 Congdon et al., 1987	
Hibernation	October late September mid-October		March-May mid-March early May	depends on latitude Iowa Ontario, Canada	Ernst & Barbour, 1972 Christiansen & Burken, 1979 Obbard & Brooks, 1981	

1 Cited in Sievert et al. (1988).
2 Estimated assuming temperature of 20°C, using equation 3-50 (Robinson et al., 1983) and body weights from Congdon et al. (1986), after subtracting 30 percent of body weight to eliminate the weight of the shell (Hall, 1924). More information on estimating energy budgets for reptiles is provided in Congdon et al. (1982).
3 Method of estimating percent diet not specified.
4 Summary of six field studies, including the author's.
5 Summary of data from various authors for eleven eutrophic ponds.
6 Cited in Petokas and Alexander (1980).
7 Cited in Graves and Anderson (1987).

8 Cited in Galbraith et al. (1989).
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2.3.2. Painted Turtle (pond and marsh turtles)

Order *Testudines*, Family *Emydidae*. Pond and marsh turtles (i.e., sliders, cooters, red-bellied turtles, and painted turtles) are small to medium-sized semiaquatic turtles well known for basking in the sun. Painted turtles are the most widespread of these in North America, ranging across the continent.

Selected species

The painted turtle (*Chrysemys picta*) is largely aquatic, living in shallow-water habitats, and is among the most conspicuous of the basking turtles. There are four subspecies in the United States (only one reaching slightly into Canada), distinguished by color variations, body size, and range: *C. p. picta* (eastern painted turtle; 11.5 to 15.2 cm; range Nova Scotia to Alabama), *C. p. marginata* (midland painted turtle; 11.5 to 14 cm; range southern Quebec and southern Ontario to Tennessee), *C. p. dorsalis* (southern painted turtle; 10 to 12.5 cm; range southern Illinois to the Gulf), and *C. p. bellii* (western painted turtle; the largest of the subspecies, 9 to 18 cm; range southwest Ontario and Missouri to the Pacific Northwest) (Conant and Collins, 1991). *C. p. dorsalis* is the smallest subspecies and also one of the smallest emydid turtles in North America (Moll, 1973). Hybridization occurs between subspecies in areas where their ranges overlap (e.g., *bellii* × *marginata* hybrids may occur in areas of Michigan) (Snow, 1980).

***Body size.* Painted turtles are medium-sized turtles (10 to 18 cm). Males are smaller than females; adult males average from 170 to 190 g, whereas adult females average from 260 to 330 g in some populations (Congdon et al., 1986; Ernst 1971b). In general, the shell comprises approximately 30 percent of the total wet weight of turtles of this size (Hall, 1924). Frazer et al. (1991) estimated a relationship between plastron length (PL in mm) and age (t in years) for a population in Michigan in the 1980's using von Bertalanffy growth equations:**

$$PL = 111.8(1 - 0.792e^{-0.184t}) \quad \text{for males, and}$$

$$PL = 152.2(1 - 0.852e^{-0.128t}) \quad \text{for females.}$$

Congdon et al. (1982) reported a relationship between plastron length (PL in mm) and body weight (Wt in grams) for painted turtles:

$$\log_e(Wt) = -6978 + 2.645 \log_e(PL).$$

Eggs weigh 4 to 6 g, and neonates retain a large yolk mass that they draw on for the first few months of life (Cagle, 1954).

***Habitat.* Painted turtle habitat requirements include soft and muddy bottoms, basking sites, and aquatic vegetation (Sexton, 1959). Painted turtles prefer slow-moving shallow water such as ponds, marshes, ditches, prairie sloughs, spring runs, canals, and occasionally brackish tidal marshes (Conant and Collins, 1991). They frequent areas with floating surface vegetation for feeding and for cover (Sexton, 1959). These areas tend to**

be warmer than more open water, which is important in the early fall as temperatures begin to drop (Sexton, 1959). For winter hibernation or dormancy, painted turtles seek deeper water (Sexton, 1959). If outlying marsh areas are dry during the summer, the turtles may return to the more permanent bodies of water sooner (McAuliffe, 1978). Painted turtles sometimes inhabit stagnant and polluted water (Smith, 1956).

Food habits. Painted turtles are omnivorous. Depending on habitat and on age, painted turtles may consume predominantly vegetation or predominantly animal matter. Marchand (1942, cited in Mahmoud and Klicka, 1979) found in one population that juveniles consumed approximately 85 percent animal matter and 15 percent plant matter, whereas the adults were primarily herbivorous, consuming 88 percent plant matter and 12 percent insects and amphipods. Knight and Gibbons (1968) found oligochaets, cladocera, dragonfly nymphs, lepidopteran larvae, and tendipedid larvae and pupae to dominate the animal component of the diet and filamentous algae to dominate the plant component of the diet in a population living in a polluted river in Michigan. Adult painted turtles in a Pennsylvania population were found to consume only 40 percent plant matter (Ernst and Barbour, 1972), whereas in a Michigan marsh and elsewhere, painted turtles of all ages apparently consumed 95 to 100 percent plant matter (Cahn, 1937, cited in Smith, 1961; Gibbons, 1967). Some carrion also may be consumed (Mount, 1975).

Temperature regulation and daily activities. Painted turtles are diurnal and usually spend their nights sleeping submerged (Ernst, 1971c). During the day, they forage in the late morning and late afternoon and bask during the rest of the day (Ernst, 1971c). Active feeding does not occur until water temperatures approach 20°C, and these turtles are most active around 20.7 to 22.4°C (Ernst, 1972; Ernst and Barbour, 1972; Hutchinson, 1979). Basking is most frequent in the spring, summer, and fall, but occasionally painted turtles bask during warm spells in the winter (Ernst and Barbour, 1972). Sexton (1959) divided the annual activity cycle of painted turtles into five parts: (1) the prevernal, which begins with the final melting of winter ice and lasts until late March, or when the turtles begin to move in mass out of the hibernation ponds; (2) the vernal, from late March to late May, when the submerged aquatic plants important to the turtles grow to the surface of the water (the initiation of feeding and mating activities and the emergence of the hatchling turtles from the nests of the previous year also occur during this season); (3) the aestival, extending from June through August, when the turtles forage, grow, nest, and return to their winter hibernation ponds; (4) the autumnal, including September through November or when a permanent ice cover forms; and (5) the winter season, which lasts while the water is permanently covered with ice.

Hibernation. Most painted turtles become dormant during the colder months but will become active during warm periods in the winter (Ernst and Barbour, 1972). *C. picta* usually hibernates in muddy bottoms of ponds (DeGraaf and Rudis, 1983). Taylor and Nol (1989) found painted turtles overwintering in an Ontario pond in areas with a mean water depth of 0.32 m (range 0.2 to 0.48 m), mean sediment depth of 0.79 m (0.5 to 0.95 m), and mean sediment temperature of 4.1°C (3 to 6°C). During hibernation, painted turtles shift toward more anaerobic metabolism, supported by glycolysis of liver and skeletal muscle glycogen (Seymour, 1982). After emerging from hibernation, the turtles convert the accumulated lactate to glucose in the liver (using aerobic metabolism) (Seymour, 1982).

Breeding activities and social organization. **Mating usually occurs in spring and summer but may continue into the fall (Ernst, 1971c; Gibbons, 1968a; Gist et al., 1990). Nesting occurs somewhat later (Cagle, 1954; Ernst and Barbour, 1972; Moll 1973). Eggs are often laid in high banks (DeGraaf and Rudis, 1983). The species does not appear to be territorial and can be found in large aggregations, particularly at favorite basking sites (Ernst, 1971c).**

Home range and resources. **In spring, as the winter ice melts, many painted turtles move away from the ponds in which they hibernated to more shallow ponds and marshes with surface vegetation (Sexton, 1959). Movements averaging 60 to 140 meters characterized one population in Michigan (Sexton, 1959). The summer home range includes the painted turtle's foraging areas and basking sites. Females find nesting sites on dry land outside of the foraging range; Congdon and Gatten (1989) found nests to average 60 meters from the edge of a foraging marsh. Females initiate nesting migrations during daylight hours, and most finish their nests before dark on the same day (Congdon and Gatten, 1989). In winter, painted turtles generally move back to the deeper ponds for hibernation (DeGraaf and Rudis, 1983).**

Population density. **Reported densities range from 11.1/ha in Saskatchewan (MacCulloch and Secoy, 1983) to 830/ha in Michigan marshes (Frazer et al., 1991). Accurate censuses are difficult, however (Bayless, 1975), and the distribution of painted turtles in summer is highly clumped, corresponding to the patches of floating aquatic vegetation (Sexton, 1959).**

Population dynamics. **Sexual maturity is attained in about 2 to 7 years, depending on the sex and size of the turtle and growing season (Christiansen and Moll, 1973; Ernst and Barbour, 1972). Males reach sexual maturity 1 to a few years earlier than females (Moll, 1973). Once sexual maturity is reached, growth of painted turtles slows or essentially ceases (Ernst and Barbour, 1972). Older, larger females tend to produce larger clutch sizes and larger eggs than younger, smaller females (Mitchell, 1985). In more southerly populations, painted turtles produce more clutches annually with fewer eggs each than in more northerly populations (Moll, 1973; Snow, 1980; Schwarzkopf and Brooks, 1986). Predation causes most nest losses, usually within the first 2 days after laying (Tinkle et al., 1981). The duration of the incubation period depends on soil temperature, and hatchlings may overwinter in the nest in more northerly populations (Gibbons and Nelson, 1978).**

Similar species (from general references)

Many species of pond and marsh turtles can be found in similar habitats; however, there are important dietary differences among species that can affect exposure to environmental contaminants, as described below. Size is listed according to carapace length, which is longer than plastron length.

cooters

- **The Florida cooter (*Pseudemys floridana*) is larger (23 to 33 cm) than the painted turtle. The *floridana* subspecies ranges from the coastal plain of**

Virginia to eastern Texas and north in the Mississippi Valley to southern Illinois, while the *peninsularis* subspecies is restricted to the Florida peninsula. The Florida cooter resides in permanent bodies of water. In their first year, young cooters feed on both aquatic plant and animal life; later they become totally herbivorous.

- **The river cooter (*Pseudemys concinna*), composed of five subspecies, also is larger (23 to 33 cm) than the painted turtle. It inhabits coastal plains ranging from southeastern Virginia to Georgia, southeast into Florida, west into Texas and New Mexico, and north in the Mississippi Valley to southern Illinois. It is chiefly a resident of streams and relatively large lakes. In their first year, young river cooters are omnivorous; the adults are almost entirely herbivorous.**

- **The Texas river cooter (*Pseudemys texana*) (18 to 25.5 cm) prefers rivers but can be found in smaller creeks and ditches. Its range is restricted to most of central and southeastern Texas.**

red-bellied turtles

- **The Florida red-bellied turtle (*Pseudemys nelsoni*) is larger (20 to 31 cm) than the painted turtle and has a range in the Florida peninsula and panhandle. It can be found basking on logs over fresh to moderately brackish water, and it prefers abundant submerged aquatic vegetation, its principal food.**

- **The Alabama red-bellied turtle (*Pseudemys alabamensis*) is larger (23 to 33 cm) than the painted turtle and is found only in the lower portion of the Mobile Bay drainage in Alabama. It prefers fresh to moderately brackish water with abundant aquatic vegetation, its principal food.**

- **The red-bellied turtle (*Pseudemys rubriventris*) is much larger (25 to 32 cm) than the painted turtle and is found in the mid-Atlantic states and eastern Massachusetts.**

sliders

- **The pond slider (*Trachemys scripta*) is similar in size or a little larger (12 to 20 cm) than the painted turtle and has three subspecies ranging from southeastern Virginia to northern Florida and west to New Mexico. During the first year, pond sliders are principally carnivorous, consuming aquatic insects, crustaceans, molluscs, and tadpoles. As they mature, sliders become herbivorous, consuming a wide variety of aquatic plants.**

- **The big bend slider (*Trachemys gaigeae*) (12 to 20 cm) is similar to the pond slider in size and habits. It is abundant locally in its limited range along the upper Rio Grande and some of its tributaries.**

General references

Behler and King (1979); Conant and Collins (1991); Congdon et al. (1986); Ernst and Barbour (1972); Moll (1973); Sexton (1959).

Painted Turtle (*Chrysemys picta*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	A F A M	266.5 ± 60.1 SD 189.1 ± 52.3 SD	83.5 - 450.3 102.0 - 274.5	Pennsylvania (*picta* x *marginata*)	Ernst, 1971b	
	A F A M J B	326.7 ± 4.95 SE 176.9 ± 1.92 SE 64.2 ± 1.59 SE		Michigan	Congdon et al., 1986	
	at hatching	3.7 ± 0.2 SD	3.5 - 3.9	central Virginia (*picta*)	Mitchell, 1985	
	at hatching	4.1 ± 0.61 SD		Iowa	Ratterman & Ackerman, 1989	
Body Length (mm plastron)	A F A M	157 ± 2.6 SE 132 ± 2.9 SE	136 - 185 96 - 155	Wisconsin (*bellii*)	Moll, 1973	
(mm plastron)	A F A M J B	125.1 ± 0.64 SE 99.9 ± 0.48 SE 65.0 ± 0.65 SE		Michigan	Congdon et al., 1986	
(mm carapace)	A F A M J B	134.2 ± 0.81 SE 109.7 ± 0.54 SE 71.5 ± 0.69 SE		Michigan	Congdon et al., 1986	
Egg Weight (g)	initial mass	6.17		Georgia (*dorsalis*)	Congdon & Gibbons, 1985	
	initial mass final mass	6.65 ± 0.67 SD 8.62 ± 1.06 SD		Iowa	Ratterman & Ackerman, 1989	
Growth Rate	J F - 1 yr J F - 2 to 3 yr J F - 4 to 5 yr J F - 6 to 7 yr A F - 8 to 12 yr A F - > 12 yr	35 mm/yr 19 - 20 mm/yr 12 mm/yr 8 - 10 mm/yr 3 - 6 mm/yr < 3 mm/yr		Quebec, Canada (*marginata*) (measured using plastron)	Christens & Bider, 1986	

Painted Turtle (*Chrysemys picta*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Metabolic Rate (lO_2/kg-d)	adults; 25°C land, rest water, swim juv.; 25°C feeding 1-day fast 10-day fast 19-day fast	 0.73 ± 0.44 SD 0.22 ± 0.32 SD 0.39 ± 0.68 SD 5.06 ± 0.42 SE 3.44 ± 0.29 SE 1.98 ± 0.13 SE 1.57 ± 0.19 SE		North Carolina NS (*marginata*)	Stockard & Gatten, 1983 Sievert et al., 1988	1 2
Metabolic Rate (kcal/d, averaged over 1 year)	J F - yr 1 J F - yr 3 J F - yr 5 J F - yr 7 A F - yr 9 A F - yr 11 A F - yr 13	0.06 0.30 0.53 0.77 1.12 1.23 1.28		Michigan (*marginata*)	Congdon et al., 1982	3
Food Ingestion Rate (g/g-d)						4
Water Ingestion Rate (g/g-d)	A B A B summer	 0.02	up to 0.025 0.016 - 0.022	Wisconsin (*bellii*) (lab) Pennsylvania (lab)	Trobec & Stanley, 1971 Ernst, 1972	5 6
Inhalation Rate (m^3/kg-d)	A B resting	0.0025 ±0.0005 SE		NS (lab)	Milsom & Chan, 1986	

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
all ages: plants		 > 95			Michigan/marsh (% wet weight; stomach contents)	Gibbons, 1967	

Painted Turtle (*Chrysemys picta*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
all ages:					Michigan/polluted river	Knight & Gibbons, 1968	
plants	31.6	38.7					
animals	77.3	72.3			(% wet weight; stomach contents)		
Oligochaeta	-	30.0					
Cladocera	1.5	48.5					
Odonata nymphs	60.0	38.3					
Lepidoptera larvae	1.0	50.0					
Tendipedidae larva	30.8	7.7					
Tendipedidae pupae	36.7	10.0					
detritus	7.8	1.9					
adults:							
snails		12.1			Pennsylvania (*picta*)/NS	Ernst & Barbour, 1972	
amphipods		3.0					
crayfish		7.5			(% wet volume; stomach contents)		
insects		11.5					
fish		13.0					
other animals		14.1			season not specified		
algae		14.7					
vascular plants		24.1					
other plants		0.8					

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Movements (m)	A B spring	63 - 144	up to 301	Michigan (*marginata*)/NS	Sexton, 1959	7
	A B summer	86 - 91	up to 300			
	A B fall	88 - 130	up to 336			
Population Density (N/ha)	B B summer	11.1		Saskatchewan, Canada (*bellii*)/river	MacCulloch & Secoy, 1983	
	B B		98 - 410	Michigan (*marginata*)/ponds, marsh	Sexton, 1959	
	B B	590	240 - 941	Pennsylvania/pond, marsh	Ernst, 1971c	
	B B	828		Michigan/lake, marsh	Frazer et al., 1991	

Painted Turtle (*Chrysemys picta*)

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Clutch Size		19.8	17 - 23	Saskatchewan, Canada (*bellii*)/creek	MacCulloch & Secoy, 1983	
		10.7	4 - 16	Wisconsin (*bellii*)/NS	Moll, 1973	
		7.6	2 - 11	Michigan (*marginata*)/NS	Congdon & Tinkle, 1982	
		4.8	2 - 9	Tennessee (*dorsalis* × *marginata*)/NS	Moll, 1973	
Clutches/Year		1 - 2	2	Ontario, Canada/NS	Schwarzkopf & Brooks, 1986	
		1 - 2	2	Michigan (*bellii* × *marginata*) /NS	Snow, 1980	
		> 2	3	Illinois (*bellii* × *marginata*) /kettle ponds	Moll, 1973	
		> 3	5	Tennessee, Louisiana (*dorsalis* and *d.* × *marginata*)/NS	Moll, 1973	
Days Incubation			65 - 80	se Pennsylvania/NS	Ernst, 1971c	
			60 - 65	se Wisconsin/NS (natural)	Ewert, 1979	
			72 - 99	nw Minnesota/NS (natural)	Ewert, 1979	
Age at Sexual Maturity (yr)	F	5 - 6		New Mexico (*bellii*)/NS	Christiansen & Moll, 1973	
	M	3				
	F	8		Wisconsin (*bellii*)/NS	Christiansen & Moll, 1973	
	M	4				
	F	6		Pennsylvania (*picta*)/NS	Ernst & Barbour, 1972	
	M	5				
	F	4 - 5		Tennessee (*dorsalis* x *marginata*)/NS	Moll, 1973	
	M	2 - 3				

Painted Turtle (*Chrysemys picta*)

Population Dynamics	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location/Habitat	Reference	Note No.
Length at Sexual Maturity (mm plastron)	M F	90 120 - 130		northern Michigan (*marginata*, *dorsalis*)/NS	Cagle, 1954	
	M F	70 120 - 125		southern Illinois (*marginata*, *dorsalis*)/NS	Cagle, 1954	
	M F	123 150	88 - 170 132 - 205	New Mexico (*bellii*)/NS	Christiansen & Moll, 1973	
Annual Mortality Rates (%)	A F A M		0 - 14 2 - 46	Saskatchewan, Canada, MI, NY, NE/NS	Zweifel, 1989	8
	A B J B	 54	4 - 6	Virginia/NS	Mitchell, 1988	8
Longevity	M F		up to 31 yrs up to 34 yrs	Michigan/marsh	Frazer et al., 1991	

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Mating	late April		mid-June	se Pennsylvania	Ernst, 1971c	
	March	April - early May	May	Michigan	Gibbons, 1968a	
		October		Ohio	Gist et al., 1990	
Nesting	June		July	se Pennsylvania	Ernst, 1971c	
	June		July	Illinois, Kansas	Smith, 1956, 1961	
	late May	June	late June	se Michigan (*marginata*)	Tinkle et al., 1981	
Hatching		late summer		se Michigan (*marginata*)	Tinkle et al., 1981	
	September		spring	Illinois (*marginata*)	Cahn, 1937	9
	August		September	Kansas (*bellii*)	Smith, 1956	
Hibernation	late October		late March	se Michigan (*marginata*)	Congdon et al., 1982	
	late October		April	Kansas (*bellii*)	Smith, 1956	

Painted Turtle (*Chrysemys picta*)

1 Average mass of test animals resting on land and in water = 215 g (79 to 395 g) and of test animals swimming and measured for existence metabolism = 143 g (79 to 297 g).
2 Average weight of juvenile turtles = 7.7 g.
3 Based on an annual energy budget estimated by the authors assuming that females lay one clutch of eggs per year after their seventh year.
4 See Chapters 3 and 4 for approaches to estimating food ingestion rates from metabolic rate and diet.
5 Uptake of water by turtles held in tap water.
6 Measured as evaporative water loss.
7 Spring: from hibernation to other ponds; summer: back to hibernation ponds; fall: to deep-water areas for hibernation.
8 Cited in Frazer et al., 1991.
9 Cited in Smith, 1961.

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2.3.3. Eastern Box Turtle (box turtles)

Order *Testudines*, Family *Emydidae*. Box turtles are the most terrestrial of the Emydid turtles, having close-fitting shells that have allowed them to adapt well to terrestrial life. They are found throughout the eastern and central United States and into the southwest. They are omnivorous.

Selected species

The eastern box turtle (*Terrapene carolina carolina*) ranges from northeastern Massachusetts to Georgia, west to Michigan, Illinois, and Tennessee (Conant and Collins, 1991). There are four subspecies of *T. carolina*, all found within the eastern United States: *T. c. carolina* (above), *T. c. major* (Gulf Coast box turtle; the largest subspecies, restricted to the Gulf Coast), *T. c. triunguis* (three-toed box turtle; Missouri to south-central Alabama and Texas), and *T. c. bauri* (Florida box turtle; restricted to the Florida peninsula and keys) (Conant and Collins, 1991).

***Body size.* The eastern box turtle is small, with adults ranging from 11.5 to 15.2 cm in length (plastron) and approximately 300 to over 400 g. Hatchlings weigh approximately 8 to 10 g. Turtles continue to grow throughout their lives; however, their growth rate slows after reaching sexual maturity (Ernst and Barbour, 1972), and growth rings are no longer discernable after 18 to 20 years (Stickel, 1978). Body fat reserves in a Georgia population averaged 0.058 to 0.060 g of fat per gram of lean dry weight from spring through fall (Brisbin, 1972).**

***Habitat.* Typical box turtle habitats include open woodlands, thickets, and well-drained but moist forested areas (Stickel, 1950), but occasionally pastures and marshy meadows are utilized (Ernst and Barbour, 1972). In areas with mixed woodlands and grasslands, box turtles use grassland areas in times of moderate temperatures and peak moisture conditions; otherwise, they tend to use the more moist forested habitats (Reagan, 1974). Many turtles are killed attempting to cross roads, and fragmentation of habitat by roads can severely reduce populations (DeGraaf and Rudis, 1983; Stickel, 1978).**

***Food habits.* Adult *T. carolina* are omnivorous (Ernst and Barbour, 1972). When young, they are primarily carnivorous, but they become more herbivorous as they age and as growth slows (Ernst and Barbour, 1972). They consume a wide variety of animal material, including earthworms, slugs, snails, insects and their larvae (particularly grasshoppers, moths, and beetles), crayfish, frogs, toads, snakes, and carrion; they also consume vegetable matter, including leaves, grass, berries, fruits, and fungi (DeGraaf and Rudis, 1983). A high proportion of snails and slugs may comprise the animal matter in the diet (Barbour, 1950), and seeds can become an important component of the plant materials in the late summer and fall (Klimstra and Newsome, 1960).**

***Temperature regulation and daily activities.* The species is diurnal and spends the night resting in a scooped depression or form that the turtle digs in the soil with its front feet (Ernst and Barbour, 1972; Stickel, 1950). *T. carolina* are most active in temperate,**

humid weather (Stickel, 1950). In the summer, they avoid high temperatures during midday by resting under logs or leaf litter, in mammal burrows, or by congregating in mudholes (Smith, 1961; Stickel, 1950). In the hottest weather, they may enter shaded shallow pools for hours or days (Ernst and Barbour, 1972). In the cooler temperatures, they may restrict their foraging activities to midday (Stickel, 1950). In the laboratory, locomotion is maximal between 24 and 32°C (Adams et al., 1989). In the field, their mean active body temperature is approximately 26°C (Brattstrom, 1965, cited in Hutchinson, 1979).

Hibernation. **In the northern parts of its range (northeastern Massachusetts, Michigan, Illinois), the eastern box turtle enters hibernation in late October or November and emerges in April. In Louisiana, Penn and Pottharst (1940, cited in Ernst and Barbour, 1972) found that *T. c. major* hibernated when temperatures fell below 65°F. To hibernate, the box turtle burrows into loose soil and debris or mud of ponds or stream bottoms. Congdon et al. (1989) found a South Carolina population of box turtles to occupy relatively shallow burrows (less than 4 cm) compared with those occupied by box turtles in colder regions (up to 46 cm). Dolbeer (1971) found hibernacula of box turtles in Tennessee to be under 15.5 cm of leaf litter and 5.8 cm of soil on average. In southern states, during rainy and warm periods, box turtles may become active again (Dolbeer, 1971). In Florida, the box turtle may be active all year (Ernst and Barbour, 1972).**

Breeding activities and social organization. **Box turtles are solitary except briefly during the mating season. Individuals restrict their activities to a foraging home range, but home ranges of different individuals can overlap substantially (Stickel, 1950). Mating usually occurs in the spring but may continue into fall, and eggs are laid in late spring and summer (Ernst and Barbour, 1972). The female digs a 3- to 4-inch cavity in sandy or loamy soil in which she deposits her eggs and then covers the nest with soil. Nests tend to be constructed several hundred meters from the female's foraging home range in the warmer and drier uplands (Stickel, 1989). The duration of incubation depends on soil temperatures, and sometimes hatchlings overwinter in the nest. The young are semiaquatic but seldom seen (Smith, 1956).**

Home range and resources. **Measures of the foraging home range for box turtles range from .5 ha to just over 5 ha (Dolbeer, 1969; Schwartz et al., 1984). A female may need to search for suitable nest site (e.g., slightly elevated sandy soils) (Ernst and Barbour, 1972) outside of her foraging home range (Stickel, 1950). Winter hibernacula tend to be within the foraging home range (Stickel, 1989).**

Population density. **Population density varies with habitat quality, but studies linking density to particular habitat characteristics are lacking. In some areas, population densities have declined steadily over the past several decades (Schwartz and Schwartz, 1974; Stickel, 1978). Some investigators attribute the decline to increasing habitat fragmentation and obstacles (e.g., highways) that prevent females from reaching or returning from appropriate nesting areas (Stickel, 1978; DeGraaf and Rudis, 1983).**

Population dynamics. **Sexual maturity is attained at about 4 or 5 years (Ernst and Barbour, 1972) to 5 to 10 years of age (Minton, 1972, cited in DeGraaf and Rudis, 1983). One to four clutches may be laid per year, depending on latitude (Oliver, 1955, cited in**

Moll, 1979; Smith, 1961). Clutch size ranges from three to eight eggs, averaging three to four in some areas (Congdon and Gibbons, 1985; Ernst and Barbour, 1972; Smith, 1956). Juveniles generally comprise a small proportion of box turtle populations, for example, 18 to 25 percent in one population in Missouri (Schwartz and Schwartz, 1974) and 10 percent in a study in Maryland (Stickel, 1950). Some individual box turtles may live over 100 years (Graham and Hutchinson, 1969, cited in DeGraaf and Rudis, 1983; Oliver, 1955, cited in Auffenberg and Iverson, 1979).

Similar species (from general references)

- **The ornate box turtle (*Terrapene ornata ornata*) and the desert box turtle (*Terrapene ornata luteola*) are similar in size and habits to the eastern box turtle. They occur in the western, midwestern, and southern midwestern states. Preferred habitats include open prairies, pastureland, open woodlands, and waterways in arid, sandy-soil terrains. The ornate box turtle and desert box turtle forage primarily on insects but also on berries and carrion.**

General references

Behler and King (1979); Conant and Collins (1991); DeGraaf and Rudis (1983); Ernst and Barbour (1972); Stickel (1950).

Eastern Box Turtle (*Terrapene carolina*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	A F fall A M fall	381 ± 29 SE 398 ± 47 SE		Georgia (*carolina*), captive	Brisbin, 1972	
	A F spring A M spring	388 ± 29 SE 369 ± 47 SE		Georgia (*carolina*)	Brisbin, 1972	
	A F	372		South Carolina	Congdon & Gibbons, 1985	
	at hatching	8.8 8.4		Florida (*major*) Indiana (*carolina*)	Ewert, 1979 Ewert, 1979	
	2 months 1.3 years 3.3 years	21 40 54		Tennessee	Allard, 1948	1
Body Fat (g/g lean dry weight)	B fall B spring B summer	0.058 ± 0.014 SE 0.060 ± 0.016 SE 0.059 ± 0.006 SE		Georgia (*carolina*), captive	Brisbin, 1972	
Length	A F A at hatching	129 mm plastron 28 mm carapace	 up to 198 mm carapace	South Carolina NS/NS NS/NS	Congdon & Gibbons, 1985 Oliver, 1955 Oliver, 1955	 2 2
Egg Weight (g)		9.02 ± 0.17 SE	 6 - 11	South Carolina NS/NS	Congdon & Gibbons, 1985 Ernst & Barbour, 1972	
Metabolic Rate (kcal/kg-d)	A F basal	5.4			estimated	3
Food Ingestion Rate (g/g-d)						4

Eastern Box Turtle (*Terrapene carolina*)

Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat (measure)	Reference	Note No.
snails crayfish plants crickets unidentified seeds		60 15 12.5 7.5 5			Kentucky (*carolina*)/ Cumberland Mountains (% volume; stomach contents)	Barbour, 1950	
plant matter insects (adults) insects (larvae) seeds Gastropoda Isopoda Diplopoda Decapoda Annelida mammals reptiles birds	35 18 4 8 18 <1 3 2 1 2 1 3	39 12 5 16 6 5 2 2 1 <1 3 1	20 12 9 33 8 3 5 0 4 2 1 <1		Illinois (*carolina*)/forest, prairie (% wet volume; digestive tract)	Klimstra & Newsome, 1960	

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/Habitat	Reference	Note No.
Home Range Size (ha)	summer	0.46		Tennessee (*carolina*)/ woodland	Dolbeer, 1969	5
	B M B F	1.2 1.1		Maryland (*carolina*)/ bottomland forest	Stickel, 1989	5
	B M B F	5.2 5.1		Missouri (*triunguis*)/mixed woods, fields	Schwartz et al., 1984	5
Population Density (N/ha)		2.8 - 3.6		Tennessee/woodland	Dolbeer, 1969	
		17 - 35		Maryland (*triunguis*)/forest	Schwartz et al., 1984	

Eastern Box Turtle (*Terrapene carolina*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/Habitat	Reference	Note No.
Clutch Size		3.4 ± 0.3 SE 4	 2 - 7	South Carolina/NS Washington, DC/NS	Congdon & Gibbons, 1985 Smith, 1956	
Clutches/Year		 1	up to 4	Florida/NS Illinois/NS	Oliver, 1955 Smith, 1961	6
Days Incubation		 99	78 - 102 69 - 161	northwest Minnesota/(natural) Washington, DC/(natural)	Ewert, 1979 Ewing, 1933	 7
Age at Sexual Maturity (yr)	B B	4 - 5 5 - 10		NS/NS NS/NS	Ernst & Barbour, 1972 Minton, 1972	 8
Length at Sexual Maturity (mm carapace)	B		100 - 130	NS/NS	Oliver, 1955	2
Longevity (yr)		20	up to 80 up to 138	NS/NS captivity	Nichols, 1939a Oliver, 1955	8 2

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Mating	 June	spring	 July	northern range ne Carolinas, Washington, DC	Ernst & Barbour, 1972 DeGraaf & Rudis, 1983; Smith, 1956	
Hatching	September August		October September	northern range ne Carolinas	Ernst & Barbour, 1972 DeGraaf & Rudis, 1983	
Hibernation	November October		April April	northern range Missouri (*triunguis*)	Ernst & Barbour, 1972 Schwartz & Schwartz, 1974	

1 Cited in Ernst and Barbour (1972).
2 Cited in Auffenberg and Iverson (1979).
3 Estimated assuming temperature of 20°C, using Equation 3-50 (Robinson et al., 1983) and body weights of Brisbin (1972) after subtracting 30 percent of the body weight to eliminate the weight of the shell (Hall, 1924).
4 See Chapters 3 and 4 for methods of estimating ingestion rates from metabolic rate and diet.

Eastern Box Turtle (*Terrapene carolina*)

5 Foraging home range; nest sites can be several hundred meters away from the foraging home range.
6 Cited in Moll (1979).
7 Cited in Ewert (1979).
8 Cited in DeGraaf and Rudis (1983).

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2.3.4. Racer (and whipsnakes)

<u>Order *Squamata*, Family *Colubridae*</u>. All racer snakes (*Coluber constrictor*) and whipsnakes (*Masticophis*) belong to the family *Colubridae*, along with 84 percent of the snake species in North America. Colubrids vary widely in form and size and can be found in numerous terrestrial and aquatic habitats. The more terrestrial members of this family also include some brown and garter snakes; lined snakes; earth snakes; hognose snakes; small woodland snakes; green snakes; speckled racer and indigo snakes; rat snakes; glossy snakes; pine, bull, and gopher snakes; kingsnakes and milk snakes; scarlet, long-nosed, and short-tailed snakes; ground snakes; rear-fanged snakes; and crowned and black-headed snakes (Conant and Collins, 1991).

Selected species

Racer snakes (*Coluber constrictor*) are slender and fast moving and are found in a wide variety of terrestrial habitats. They are one of the most common large snakes in North America (Smith, 1961). There are 11 subspecies in North America, limited to the United States and Mexico: *C. c. constrictor* (northern black racer; southern Maine to northeastern Alabama), *C. c. flaviventris* (eastern yellowbelly racer; Montana, western North Dakota, and Iowa south to Texas), *C. c. foxii* (blue racer; northwest Ohio to eastern Iowa and southeast Minnesota), *C. c. anthicus* (buttermilk racer; south Arkansas, Louisiana, and east Texas), *C. c. etheridgei* (tan racer; west-central Louisiana and adjacent Texas), *C. c. helvigularis* (brownchin racer; lower Chipola and Apalachicola River Valleys in Florida panhandle and adjacent Georgia), *C. c. latrunculus* (blackmask racer; southeast Louisiana along east side of Mississippi River to northern Mississippi), *C. c. mormon* (western yellow-bellied racer; south British Colombia to Baja California, east to southwest Montana, western Wyoming, and western Colorado), *C. c. oaxaca* (Mexican racer; south Texas and Mexico), *C. c. paludicola* (Everglades racer; southern Florida Everglades region and Cape Canaveral area), and *C. c. priapus* (southern black racer; southeastern states and north and west in Mississippi Valley).

***Body size*. Adult racer snakes are usually 76 to 152 cm in total length (Conant and Collins, 1991). Brown and Parker (1984) developed an empirical relationship between snout-to-vent length (SVL)[i] and body weight for male and female racers of the *mormon* subspecies in northern Utah:**

weight (g) = -100.80 + 2.93 SVL (cm) females,[j] and

weight (g) = -82.65 + 2.57 SVL (cm) males.

The equations apply only over a limited range of body sizes (40 to 70 cm) where the relationship is approximately linear instead of exponential. Kaufman and Gibbons (1975)

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[i]Measures of SVL exclude the tail. Fitch (1963) estimated that the tail measures 28 percent of the SVL of young females and 31 percent of the SVL of young males.
[j]Females collected when nonreproductive.

determined a relationship between length and weight for both sexes of a South Carolina population:

$$\text{weight (g)} = 0.0003\ \text{SVL (cm)}^{2.97\ (\pm 0.15\ 2SE)} \qquad \text{both sexes.}^{k}$$

Racers from populations in the northeastern United States tend to be the largest, while those from the far west and south Texas are the smallest (Fitch, 1963). Just prior to egg-laying, the eggs can account for over 40 percent of a gravid female's body weight (Brown and Parker, 1984). At hatching, racers weigh about 8 or 9 g. Weight gain during the first year is rapid, with both sexes increasing their weight after hatching by approximately 3.2 times in the first year (Brown and Parker, 1984). One-year-old females nearly double their weight during their second year (Brown and Parker, 1984). By the time females are 3 years old (when most reach sexual maturity), they are 1.3 times heavier than the males (Brown and Parker, 1984).

***Habitat*.** Racers can be found in moist or dry areas, abandoned fields, open woodlands, mountain meadows, rocky wooded hillsides, grassy-bordered streams, pine flatwoods, roadsides, and marshes from sea level to 2,150 m in elevation (Behler and King, 1979). Racers are partially arboreal (Behler and King, 1979; DeGraaf and Rudis, 1983). *C. c. constrictor* seems to prefer forest edges and open grassy, shrubby areas (Fitch, 1963, 1982). In autumn, most *C. constrictor* move into woodlands to find rock crevices in which to overwinter (Fitch, 1982).

***Food habits*.** Racers are foraging generalists that actively seek their prey. Their varied diet includes small mammals (e.g., mice, voles), insects, amphibians (especially frogs), small birds, birds' eggs, snakes, and lizards (Brown and Parker, 1982; Fitch, 1963; Klimstra, 1959). In early spring, *C.c. flaviventris* feeds primarily on mammals and from May to October feeds primarily on insects (Klimstra, 1959). They often capture new prey before fully digesting previously captured prey (Fitch, 1982). Females, which are larger than males, tend to consume a higher proportion of vertebrate prey than do the males (Fitch, 1982). Males tend to spend more time climbing among foliage in low shrubs and trees and consuming insects (Fitch, 1982).

***Temperature regulation and daily activities*.** *C. constrictor* is diurnal and spends a good portion of the daylight hours foraging (Vermersch and Kuntz, 1986). The species is fast moving and may be encountered in almost any terrestrial situation (Fitch, 1982). Hammerson (1987) observed California racers to bask in the sun after emerging from their night burrows or crevices until their internal body temperature reached almost 34°C, after which they would begin actively foraging. When temperatures are moderate, racers will spend much of their time during the day in the open above ground; at high temperatures, racers may retreat underground (Brown and Parker, 1982). Although racers are good climbers, they spend most of their time on the ground (Behler and King, 1979). When searching for food or being pursued, the racer snake will not hesitate to climb or swim (Smith, 1961).

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[k] 95 percent confidence interval for constant (intercept in log-transform regression) = 0.00015 to 0.00058.

***Hibernation*.** **In fall, racers move to their hibernacula fairly directly and begin hibernation soon thereafter (Brown and Parker, 1982; Fitch, 1963). Racers hibernate in congregations of tens to hundreds of snakes (Brown and Parker, 1984), sometimes with copperheads and rattlesnakes, often using deep rock crevices or abandoned woodchuck holes (Parker and Brown, 1973). They are among the earliest snakes to emerge from hibernation (DeGraaf and Rudis, 1983).**

***Breeding activities and social organization*.** **The species breeds in the spring or early summer. Racers defend home territories (DeGraaf and Rudis, 1983; Smith, 1956). Eggs are laid in the summer in rotting wood, stumps, decaying vegetable matter, or loose soil and hatch about 2 months later (Behler and King, 1979; DeGraaf and Rudis, 1983). More than one male may mate with one female in a breeding season. Eggs may double in size before hatching by absorbing water from the surrounding soil (Fitch, 1963).**

Home range and resources*.** ***C. c. constrictor **appears to have a definite home range (Smith, 1956) and requires large tracts of mixed old fields and woodlands (M. Klemens, pers. comm., cited in DeGraaf and Rudis, 1983). Fitch (1963) described four types of movement depending on the season and activity: (1) those in areas where hibernation occurs (e.g., rocky ledges), (2) seasonal migration between hibernation and summer ranges during spring and fall, (3) daily activities within a home range during the active season, and (4) wandering movements during which the racer shifts its activities.**

***Population density*.** **Population densities of between 0.3 and 7 active snakes per hectare have been recorded in different habitats and areas (Fitch, 1963; Turner, 1977). Data on population densities are limited due to the difficulty in accurately censusing snakes.**

***Population dynamics*.** **Male racers can reach sexual maturity by 13 to 14 months, whereas females tend not to mature until 2 or 3 years of age (Behler and King, 1979; Brown and Parker, 1984). Adult females produce at most a single clutch each year (some may reproduce only in alternate years) (Fitch, 1963). In general, the number of eggs in a clutch is proportional to the size of the female and ranges from 4 to 30 eggs (Fitch, 1963). Incubation lasts approximately 40 days to 2 months, depending on temperature (Behler and King, 1979; Smith, 1956). Juvenile snakes suffer higher mortality rates (e.g., 80 percent) than adult snakes (e.g., 20 percent) (Brown and Parker, 1984).**

Similar species (from general references)

- **The eastern coachwhip (*Masticophis flagellum flagellum*) (black phase) is similar in size and ranges from North Carolina and south Florida to Texas, Oklahoma, and Kansas.**

- **The western coachwhip (*Masticophis flagellum testaceus*) is similar in size to the racer. It ranges from western Nebraska south to Mexico.**

- **The central Texas whipsnake (*Masticophis taeniatus girardi*), Schott's whipsnake (*Masticophis taeniatus schotti*), and Ruthven's whipsnake**

(*Masticophis taeniatus ruthveni*) are all similar in size to the racer and are restricted to southern Texas and northern Mexico.

- The Sonora whipsnake (*Masticophis bilineatus*) can be slightly larger (76 to 170 cm) than the racer and is found from Arizona southwest to New Mexico and Mexico.

- The striped racer (*Masticophis lateralis*) is also similar in size to the racer snake. It ranges from south-central Washington southeast in Great Basin to southern New Mexico and western and central Texas, south to west-central Mexico.

- The desert striped whipsnake (*Masticophis taeniatus taeniatus*) is similar to the central Texas whipsnake. It ranges from northern Texas and northern California to Washington state.

General references

Behler and King (1979); Brown and Parker (1984); Conant and Collins (1991); DeGraaf and Rudis (1983); Fitch (1963).

Racer Snake (*Coluber constrictor*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	males: yrs/mm SVL			Utah (*mormon*)	Brown & Parker, 1984	
	<1 266	8.3				
	1 420	27.0				
	2 486	41.0				
	3 520	49.1				
	4 541	53.4				
	5 564	60.4				
	6 573	61.2				
	females: yrs/mm SVL			Utah (*mormon*)	Brown & Parker, 1984	
	<1 272	8.8				
	1 430	28.4				
	2 524	51.6				
	3 575	66.2				
	4 599	71.4				
	5 620	79.4				
	6 632	84.0				
	males: yrs/mm SVL			Kansas (*flaviventris*)	Fitch, 1963	
	2 615	68.2				
	3 706	102.1				
	4 757	139.0				
	5 806	152.4				
	6 827	175.9				
	7 845	181.2				
	8 868	217.5				

Racer Snake (*Coluber constrictor*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g) (continued)	females: yrs/mm SVL 2 644 3 810 4 866 5 914 6 965 7 974	 83.5 149.4 212.3 209.6 245.9 251.3		Kansas (*flaviventris*)	Fitch, 1963	
	neonate 215 mm SVL	4.16	2.4 - 5.8	Kansas (*flaviventris*)	Fitch, 1963	
Egg Weight (g)	female size: 892 mm SVL 773 mm SVL	 5.5 4.9	 4.4 - 6.0 4.4 - 5.2	Kansas (*flaviventris*)	Fitch, 1963	
	size NS	7.8 ± 0.17 SE	5.9 - 10.8	Utah (*mormon*)	Brown & Parker, 1984	
Juvenile Growth Rate (g/d)	both sexes; 0 to 10 wks	0.116		Kansas (*flaviventris*)	Fitch, 1963	1
Body Temperature (°C)	A B summer	31.8 ± 0.20 SE	18.6 - 37.7	Utah (*mormon*)	Brown, 1973	2
	A B summer	26 - 27 (mode)	15.5 - 32.4	Kansas (*flaviventris*)	Fitch, 1963	
Metabolic Rate (kcal/kg-d)	M basal F basal	6.78 6.19			estimated	3
Food Ingestion Rate (g/g-d)	B B: spring through fall	0.02		Kansas (*flaviventris*)	Fitch, 1982	4

Racer Snake (*Coluber constrictor*)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
insects	20	40	64		s Illinois/pastures, meadows	Klimstra, 1959	5
small mammals	62	27	21				
amphibians	5	13	3		(% volume; digestive tracts)		
reptiles	7	8	-				
birds	4	6	8				
other	2	6	4				
small mammals		65.7			Kansas (*flaviventris*)/ locations throughout state	Fitch, 1963	
orthopterans		14.3					
lizards		9.2					
snakes		4.2			(% wet weight; scats and stomach contents)		
misc. insects		1.9					
birds		3.5					
frogs		1.2					
mice		15.4			Kansas (*flaviventris*)/ woodland, grassland	Fitch, 1963	
orthopterans		4.6					
lizards		61.5					
frogs		12.6			(% wet weight; stomach contents)		
snakes		5.1					
crickets		0.8					

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/ Habitat	Reference	Note No.
Home Range Size (ha)	A F summer A M summer	1.8 3.0		Kansas (*flaviventris*)/ woodland, grassland	Fitch, 1963	
Population Density (N/ha)	A B summer	7.0		Kansas (*flaviventris*)/ upland prairie, weeds, grasses	Fitch, 1963	
	B B	0.32		Utah (*mormon*)/desert shrub	Brown & Parker, 1984	

Racer Snake (*Coluber constrictor*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/ Habitat	Reference	Note No.
Clutch Size	average average average	16.8 12.6 5.28 ± 0.24 SE	7 - 31 7 - 21 4 - 8	NS (*constrictor*)/NS NS (*priapus*)/NS Utah (*mormon*)/desert shrub	Fitch, 1963 Fitch, 1963 Brown & Parker, 1984	6 6
Clutches/Year		0.5	up to 1	Kansas (*flaviventris*)/ woodland, grassland	Fitch, 1963	
Days Incubation	summer summer	51 45 - 50	43 - 63	Kansas (*flaviventris*)/lab Utah (*mormon*)/desert	Fitch, 1963 Brown & Parker, 1984	
Age at Sexual Maturity	F M	2 - 3 years 13 - 14 months		Kansas (*flaviventris*)/ woodland, grassland	Fitch, 1963	
Annual Mortality Rates (%)	B 2 yrs B 3 - 6 yrs B 7 yrs	58 25 - 30 38		Kansas (*flaviventris*)/ woodland, grassland	Fitch, 1963	
Longevity (yr)	A B		up to 20	Utah (*mormon*)/cold desert shrub	Brown & Parker, 1982	

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Mating	April May April	May	June early June May	Kansas (*flaviventris*) NS (*constrictor*) Texas (*flaviventris*)	Fitch, 1963 DeGraaf & Rudis, 1983 Vermersch and Kuntz, 1986	
Nesting	June June		July early August	Virginia, Carolinas Texas (*flaviventris*)	Martof et al., 1980 Vermersch and Kuntz, 1986	
Hatching	late August 	 mid-late August	early September 	Kansas (*flaviventris*) Utah (*mormon*)	Fitch, 1963 Brown & Parker, 1982	

Racer Snake (*Coluber constrictor*)

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Hibernation	late November		early April	Kansas (*flaviventris*)	Fitch, 1963	
	early October		early May	Utah (*mormon*)	Brown & Parker, 1982	

1 Ten-week period from hatching to hibernation.
2 Active snakes under natural conditions; cited in Brown and Parker (1982).
3 Estimated assuming temperature of 20°C using Equation 3-50 (Robinson et al., 1983) and body weights of 3-year-old snakes from Fitch (1963).
4 Author estimated that the snakes eat approximately four times their body weight over the 213-day active season from spring through fall.
5 Size of snakes not specified; captured within the range of *C. c. flaviventris* and *C. c. priapus*.
6 Author summarizing own work and unspecified other studies.

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2.3.5. Northern Water Snake (water snakes and salt marsh snakes)

<u>Order *Squamata*, Family *Colubridae*</u>. Water snakes and salt marsh snakes (genus *Nerodia*) belong to the family *Colubridae*, along with 84 percent of the snake species in North America. Colubrids vary widely in form and size and can be found in numerous habitats, including terrestrial, arboreal, aquatic, and burrowing. The more aquatic types of snakes in this family include water snakes, salt marsh snakes, swamp snakes, brown snakes, and garter and ribbon snakes (Conant and Collins, 1991).

Selected species

The northern water snake (*Nerodia sipedon sipedon*) is largely aquatic and riparian. It ranges from Maine and southern Quebec to North Carolina. It also inhabits the uplands of western North Carolina and adjacent portions of Tennessee and Virginia, and its range extends west to eastern Colorado (Conant and Collins, 1991). Three additional subspecies are recognized, distinguished by range and habitat: *N. s. pleuralis* (midland water snake; ranges from Indiana to Oklahoma and the Gulf of Mexico and south of the mountains to the Carolinas, preferring fast-moving streams), *N. s. insularum* (Lake Erie water snake; inhabits islands of Put-in-Bay, Lake Erie), and *N. s. williamengelsi* (Carolina salt marsh water snake; inhabits the Outer Bank islands and mainland coast of Pamlico and Core sounds, North Carolina) (Behler and King, 1979; Conant and Collins, 1991).

***Body size*. The northern water snake is typically 61 to 107 cm in total length (Conant and Collins, 1991). Island populations of the species tend to be larger than mainland ones (King, 1986). King (1986) estimated the relationship between snout-to-vent length (SVL)[l] and body weight for Lake Erie water snakes (*N. s. insularum*):**

weight (g) = 0.0005 SVL (cm)$^{3.07}$	**all snakes;**
weight (g) = 0.0009 SVL (cm)$^{2.88}$	**females; and**
weight (g) = 0.0008 SVL (cm)$^{2.98}$	**males.**

Kaufman and Gibbons (1975) determined a relationship between length and weight for both sexes of a South Carolina population:

weight (g) = 0.0004 SVL (cm)$^{3.15\ (\pm\ 0.12\ SE)}$	**all snakes**

(95% CI for intercept = 0.00015 to 0.0011). Immediately after emergence from hibernation, females begin to gain weight and continue gaining weight until giving birth in late summer. Weight loss associated with parturition in one population ranged from 28.2 to 45.5 percent of the female's weight just prior to parturition (King, 1986).

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[l]Measures of SVL exclude the tail. Kaufman and Gibbons (1975) estimated that the tail represents 21.8 percent (± 0.010 SE) of the total length of a female and 25.7 percent (± 0.006 SE) of the total length of a male.

***Habitat*.** **The northern water snake prefers streams but can be found in lakes and ponds and nearby riparian areas (King, 1986; Smith, 1961). In the Carolinas and Virginia, they can be found from mountain lakes and streams to large coastal estuaries (Martof et al., 1980). They are absent from water bodies with soft muddy bottoms which may interfere with foraging (Lagler and Salyer, 1945). In Lake Erie, *N. s. insularum* occurs in shoreline habitats where rocks or vegetation provide refugia (King, 1986).**

***Food habits*.** **Northern water snakes consume primarily fish and amphibians and, to a lesser extent, insects and small mammals (Raney and Roecker, 1947; Smith, 1961). Diet varies according to the age (and size) of the snake and food availability (DeGraaf and Rudis, 1983). Young snakes forage in shallow riffles and cobble bars, primarily waiting for prey to move within range (letter from K.B. Jones, U.S. Environmental Protection Agency Environmental Monitoring Systems Laboratory, to Susan B. Norton, January 6, 1992). Tadpoles comprise a large proportion of the diet of young snakes[m] in some areas (Raney and Roecker, 1947). Adults are strong swimmers and can swim and dive for fish midstream, often capturing large specimens (e.g., 20 to 23 cm brown trout; 19 cm bullhead; 20+ cm lamprey) (Lagler and Salyer, 1945). They also tend to consume bottom-dwelling fish species (e.g., suckers) (Raney and Roecker, 1947). In New York, Brown (1958) found that *N. s. sipedon* consumed the most food between June and August; they consumed little during the remaining months prior to hibernation.**

***Temperature regulation and daily activities*.** **The northern water snake is active both day and night but is most active between 21 and 27°C (Brown, 1958; Smith, 1961). During the day, they are found in areas that provide basking sites and are not found in heavily shaded areas (DeGraaf and Rudis, 1983; Lagler and Salyer, 1945). They may become inactive and seek shelter, however, if temperatures exceed 27°C (Brown, 1958; Lagler and Salyer, 1945). They become torpid at temperatures less than 10°C (Brown, 1958).**

***Hibernation*.** **In autumn, the *N. sipedon* leaves the aquatic habitats to overwinter in rock crevices or in banks nearby (DeGraaf and Rudis, 1983; Fitch, 1982).**

***Breeding activities and social organization*.** **The northern water snake breeds primarily in early spring, and the young are born from late summer to fall (i.e., viviparous) (DeGraaf and Rudis, 1983). The rate of development before hatching is temperature dependent (Bauman and Metter, 1977).**

***Home range and resources*.** **The northern water snake usually stays in the same area of a stream, in the same pond, or in an adjacent pond for several years (Fraker, 1970). Snakes along streams have larger home ranges than snakes in ponds and lakes (Fraker, 1970). Fraker (1970) found that for large ponds (e.g., 1,500 to 2,000 m^2), the home range of an individual snake is essentially the entire pond. In fish hatcheries with smaller ponds, individual snakes frequent more than one pond (Fraker, 1970).**

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[m]Snakes less than 36 cm in length for this example.

***Population density*. Population density estimates for water snakes usually are expressed relative to a length of shoreline. Values from 34 to 380 snakes per km of shoreline have been reported for streams and Lake Erie islands (see table).**

***Population dynamics*. Northern water snakes reach sexual maturity at 2 or 3 years of age, with males generally maturing earlier and at a smaller size than females (Feaver, 1977, cited in King, 1986; King, 1986). Clutch sizes vary from 5 or 10 to 50 or 60 depending on location and on female size (see table). The proportion of females breeding in a given year increases with increasing female size, as does clutch size and offspring weight (King, 1986). King determined the relationship of litter size to female SVL for Lake Erie water snakes (*N. s. insularum*):**

litter size = -12.45 + 0.41 SVL (cm).

Feaver (1977, cited in King, 1986) determined the relationship for a Michigan population:

litter size = -23.55 + 0.55 SVL (cm).

Females produce only one clutch per year (Beatson, 1976). Information on annual survivorship of juveniles or adults was not identified in the literature reviewed.

Similar species (from general references)

- **The Mississippi green water snake (*Nerodia cyclopion*) can be slightly larger (76 to 114 cm) than the northern water snake and is found in quiet waters of the Mississippi Valley.**

- **The blotched water snake (*Nerodia erythrogaster transversa*) is larger than the northern water snake (76 to 122 cm) and is found in western Missouri and Kansas to northeastern Mexico.**

- **The northern copperbelly (*Nerodia erythrogaster neglecta*) is larger than the northern water snake (76 to 122 cm) and ranges from western Kentucky to southeastern Illinois and to Michigan.**

- **The redbelly water snake (*Nerodia erythrogaster erythrogaster*) of the midwestern United States is close in size to the water snake. It is best suited to swampy areas and sluggish streams.**

- **The yellowbelly water snake (*Nerodia erythrogaster flavigaster*) is found in the lower Mississippi Valley and adjacent areas. Like the redbelly, it is similar in size to the water snake and likely to be found in swampy areas and sluggish streams.**

- **The banded water snake (*Nerodia fasciata fasciata*) is similar in size, and its range includes the coastal plain, North Carolina to Mississippi.**

- **The broad banded water snake (*Nerodia fasciata confluens*) (56 to 90 cm) occurs in the Mississippi River delta region in marshes, swamps, and shallow waters, including brackish waters along the Gulf Coast.**

- **The Florida water snake (*Nerodia fasciata pictiventris*) is similar in size to the northern water snake and ranges from the extreme southeast of Georgia to the southern tip of Florida. It lives primarily in shallow freshwater habitats.**

- **Harter's water snake (*Nerodia harteri*) is relatively small (51 to 76 cm) and is found in central Texas.**

- **The diamondback water snake (*Nerodi rhombifer rhombifer*) can be slightly longer (76 to 122 cm) than the northern water snake and is more thick-bodied than most *Nerodia.* Its range extends south from the Mississippi Valley into Mexico.**

- **The Gulf salt marsh snake (*Nerodia clarkii clarkii*) inhabits the Gulf Coast from west-central Florida to southern Texas. It is abundant in coastal salt meadows, swamps, and marshes.**

- **The Atlantic salt marsh snake (*Nerodia clarkii taeniata*) is restricted to Volusia County along the Atlantic Coast of north Florida.**

- **The mangrove salt marsh snake (*Nerodia clarkii compressicauda*) is small (38 to 76 cm) and inhabits the mangrove swamps of Florida's lower coasts.**

Dietary differences are evident among these species. Mushinsky et al. (1982) found in Louisiana forested wetlands that *N. erythrogaster* and *N. fasciata* change from a diet of fish to one dominated by frogs when they exceed an SVL of 50 cm. *N. rhombifer* and *N. cyclopion*, on the other hand, consume primarily fish throughout their lives, although the species and size composition of their diet changes as they grow larger (Mushinsky et al., 1982). *As N. rhombifer* exceeds 80 cm SVL, it begins to prey upon larger fish that occupy deeper open-water habitats. *N. cyclopion* eats a larger proportion of centrarchid fish as its body size increases. In a study of the diet of *N. rhombifer*, Plummer and Goy (1984) found a relationship between the SVL of the snakes and the standard length (SL) of the fish prey (defined as 80 percent of total length):

$$SL_{fish}\ (cm) = -5.9 + 0.23\ SVL_{snake}\ (cm) \qquad \text{for males, and}$$

$$SL_{fish}\ (cm) = -3.6 + 0.17\ SVL_{snake}\ (cm) \qquad \text{for females.}$$

The regression lines are not significantly different, however.

General references

Behler and King (1979); Conant and Collins (1991); DeGraaf and Rudis (1983); King (1986).

Water Snake (*Nerodia sipedon*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight **(g)**	A B	207	up to 480	Kansas	Fitch, 1982	
	J B 1 yr J B 2 yr J M 3 yr A B 5 - 6 yr	7.0 ± 2.3 SD 29.0 (N = 2) 53.2 (N = 1) 210.0 ± 65 SD	5.3 - 10.4 25.2 - 32.7 114 - 255	New York (*sipedon*)	Brown, 1958	
	neonate B	4.8	3.6 - 6.6	Ohio, Ontario (*insularum*)	King, 1986	
Length **(mm)**	A M A F	620 SVL 745 SVL		Ohio, Ontario (*insularum*)	King, 1989	1
	J B 1 yr J B 2 yr J M 3 yr A B 5 - 6 yr	285 total 496 total 607 total 868 total		New York (*sipedon*)	Brown, 1958	2
	neonate	181 SVL	125 - 210 SVL	Ohio, Ontario (*insularum*)	King, 1986	1
Juvenile Growth Rate **(g/d)**	J 1 yr J 2 yr J 3 yr	0.18 ± 0.08 SD 0.42 0.80	0.13 - 0.27 0.40 - 0.45	New York (*sipedon*)	Brown, 1958	
Metabolic Rate **(lO_2/kg-d)**	B resting: 15°C 25°C 35°C	 0.607 ± 0.035 SE 3.29 ± 0.10 SE 7.33 ± 0.23 SE	 0.39 - 0.94 2.81 - 4.44 5.70 - 9.99	Oklahoma, *Nerodia rhombifera* (similar species)	Gratz & Hutchinson, 1977	
Food Ingestion Rate **(g/g-d)**	J B 1 yr J B 2 yr J M 3 yr A B 5 - 6 yr	0.088 0.043 0.043 0.061		New York (*sipedon*)	Brown, 1958	3
Surface Area **(cm^2)**	155 mm SVL	131.16		Arkansas, *Nerodia rhombifera* (similar species)	Baeyens & Rountree, 1983	

Water Snake (*Nerodia sipedon*)

Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat (measure)	Reference	Note No.
Esocidae Catostomidae Percidae Proteidae Cyprinidae Centrarchidae crawfish		7.0 22.5 15.7 51.9 1.5 0.3 1.5			Georgia/aquatic (NS) (% wet volume; stomach contents) season not specified	Camp et al., 1980	
trout non-trout fish unidentified fish Crustacea Amphibia birds & mammals unidentified		64 7 1 1 14 12 1			n lower Michigan/streams (% wet weight; stomach contents)	Alexander, 1977	4
minnows darters Amphibia sculpin (Cottidae) trout perch (Percopsis) game fishes (Perca) burbot (Lota) catfish (Ictaluridae)			9.1 1.4 52.8 2.2 2.8 14.1 17.4 0.3		n lower Michigan/lakes (% volume; stomach contents)	Brown, 1958	5

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/ Habitat	Reference	Note No.
Population Density (N/km shore)	A B B B summer	138 34 - 41	22 - 381	Ohio, Ontario (*insularum*)/ Lake Erie islands Kansas (*sipedon*)/stream	King, 1986 Beatson, 1976	

Water Snake (*Nerodia sipedon*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/ Habitat	Reference	Note No.
Litter Size		11.8	4 - 24	Michigan (*sipedon*)/ponds, marshes	Feaver, 1977	6
		20.8 ± 8.2 SD	6 - 34	Ohio, Ontario (*insularum*)/ Lake Erie islands	Camin & Ehrlich, 1958	
		22.9	9 - 50	Ohio, Ontario (*insularum*)/ Lake Erie islands	King, 1986	
		33	13 - 52	Illinois (*pleuralis*)/NS	Smith, 1961	
Litters/Year		1		central Missouri (*sipedon*)/fish hatchery	Bauman & Metter, 1977	
		1		Kansas (*sipedon*)/stream	Beatson, 1976	
Days Gestation		58		central Missouri (*sipedon*)/fish hatchery	Bauman & Metter, 1977	
Age at Sexual Maturity (d)	F M	34 mo 23 - 24 mo		Michigan (*sipedon*)/ponds, marshes	Feaver, 1977	6
	F M	3 yrs 2 yrs		Ohio, Ontario (*insularum*)/ Lake Erie islands	King, 1986	
Length at Sexual Maturity (mm SVL)	F M		476 - 649 375 - 425	Michigan (*sipedon*)/ponds, marshes	Feaver, 1977	6
	F M	590 430		Ohio, Ontario (*insularum*)/ Lake Erie islands	King, 1986	

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Mating		April - May		Kansas (*sipedon*)	Smith, 1956	
		May		Michigan (*sipedon*)	Feaver, 1977	6
	mid-May		mid-June	central Missouri (*sipedon*)	Bauman & Metter, 1977	

Water Snake (*Nerodia sipedon*)

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Parturition	late August mid-August	 late summer	September late September	Illinois (*sipedon*) Ohio, Ontario (*insularum*) Virginia, Carolinas (*sipedon*)	Smith, 1961 King, 1986 Martof et al., 1980	
Hibernation	mid-October November		mid-April late March	Ohio, Ontario (*insularum*) Michigan (*sipedon*)	King, 1986 Feaver, 1977	 6

1 SVL = snout-to-vent length, which excludes the tail beyond the vent.
2 Total = total length, from nose to tip of tail.
3 Snakes in captivity; mean temperatures = 23°C. Snakes fed fish (one fed frogs).
4 Collected whenever they were found; thought to be active in area from May to September.
5 Months of collection and size of snakes not specified.
6 Cited in King (1986).

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2.3.6. Eastern Newt (salamanders)

<u>Order *Caudata*, Family *Salamandridae*</u>. ***Notophthalmus*, the genus comprising the eastern newts, inhabits eastern North America. A different genus, *Taricha*, comprises the western newts along the Pacific coast of North America. Unlike other salamanders, the skin of newts is rough textured, not slimy. Eastern newts are primarily aquatic; western newts are terrestrial. The life cycle of eastern newts is complex. Females deposit their eggs into shallow surface waters. After hatching, the larvae remain aquatic for 2 to several months before transforming into brightly colored terrestrial forms, called efts (Healy, 1974). Postlarval migration of efts from ponds to land may take place from July through November, but timing varies between populations (Hurlbert, 1970). Efts live on land (forest floor) for 3 to 7 years (Healy, 1974). They then return to the water and assume adult characteristics. In changing from an eft to an adult, the newt develops fins and the skin changes to permit aquatic respiration (Smith, 1961). Occasionally newts omit the terrestrial eft stage, especially in the species located in the southeast coastal plain (Conant and Collins, 1991) and along the Massachusetts coast (Healy, 1974). These aquatic juveniles have the same adaptations (i.e., smooth skin and flattened tail) as the aquatic adults but are not sexually mature (Healy, 1973). Under favorable conditions, adults are permanently aquatic; however, adults may migrate to land after breeding due to dry ponds, high water temperatures, and low oxygen tension (Hurlbert, 1969). The life cycle of western newts does not include the eft stage (Conant and Collins, 1991).**

Selected species

The eastern newt (*Notophthalmus viridescens*) has both aquatic and terrestrial forms. The aquatic adult is usually yellowish-brown or olive-green to dark brown above, yellow below. The land-dwelling eft is orange-red to reddish-brown, and its skin contains tetrodotoxin, a neurotoxin and powerful emetic. There are four subspecies of eastern newts: *N. v. viridescens* (red-spotted newt; ranges from Nova Scotia west to Great Lakes and south to the Gulf states), *N. v. dorsalis* (broken-striped newt; ranges along the coastal plain of the Carolinas), *N. v. louisianensis* (central newt; ranges from western Michigan to the Gulf), and *N. v. piaropicola* (peninsula newt; restricted to peninsular Florida) (Conant and Collins, 1991). Neoteny[n] occurs commonly in the peninsula and broken-striped newts. In the central newt, neoteny is frequent in the southeastern coastal plain. In the red-spotted newt, neoteny is rare (Conant and Collins, 1991).

***Body size*. Adult eastern newts usually are 6.5 to 10.0 cm in total length (Conant and Collins, 1991). In North Carolina, *N. v. dorsalis* efts ranged from 2.1 to 3.8 cm snout-to-vent length (SVL), which excludes the tail, and adults ranged from 2.0 to 4.4 cm SVL (Harris, 1989; Harris et al., 1988). Healy (1973) found aquatic juveniles 1 year of age to range from 2.0 to 3.2 cm SVL. Adult eastern newts weigh approximately 2 to 3 g (Gill, 1979; Gillis and Breuer, 1984), whereas the efts generally weigh 1 to 1.5 g (Burton, 1977; Gillis and Breuer, 1984).**

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[n]Neotenic newts are mature and capable of reproduction but retain the larval form, appearance, and habits (Conant and Collins, 1991).

***Habitat*.** **Larval and adult eastern newts are found in ponds, especially those with abundant submerged vegetation, and in weedy areas of lakes, marshes, ditches, backwaters, and pools of shallow slow-moving streams or other unpolluted shallow or semipermanent water. Terrestrial efts inhabit mixed and deciduous forests (Bishop, 1941, cited in Sousa, 1985) and are found in moist areas, typically under damp leaves, brush piles, logs, and stumps, usually in wooded habitats (DeGraaf and Rudis, 1983). Adequate surface litter is important, especially during dry periods, because efts seldom burrow (Healy, 1981, cited in Sousa, 1985).**

***Food habits*.** **Adult eastern newts are opportunistic predators that prey underwater on worms, insects and their larvae (e.g., mayfly, caddisfly, midge, and mosquito larvae), small crustaceans and molluscs, spiders, amphibian eggs, and occasionally small fish. Newts capture prey at the surface of the water and on the bottom of the pond, as well as in the water column (Ries and Bellis, 1966). The shed skin (exuvia) is eaten and may comprise greater than 5 percent of the total weight of food items of both the adult and eft diets (MacNamara, 1977). Snails are an important food source for the terrestrial eft (Burton, 1976). Efts feed only during rainy summer periods (Behler and King, 1979; Healy, 1973). Healy (1975) noted that in late August and September, efts often were found clustered around decaying mushrooms feeding on adult and larval dipterans. In a northern hardwood hemlock forest in New York, MacNamara (1977) found that most prey of adult migrants and immature efts were from the upper litter layer, soil surface, or low vegetation.**

***Temperature regulation and daily activities*.** **Adult newts are often seen foraging in shallow water, and efts are often found in large numbers on the forest floor after it rains (Behler and King, 1979). Efts may be found on the open forest floor even during daylight hours (Conant and Collins, 1991), but they rarely emerge if the air temperature is below 10°C (Healy, 1975).**

Hibernation. **Most adults remain active all winter underwater on pond bottoms or in streams (DeGraaf and Rudis, 1983). Some adults overwinter on land (Hurlbert, 1970) and migrate to ponds during the spring to breed (Hurlbert, 1969). If the water body freezes to the bottom, adults may be forced to hibernate on land or to migrate to another pool (Smith, 1956). Efts hibernate on land, burrowing under logs and debris. Hurlbert (1969) observed that efts migrated to ponds for the first time in the spring and fall.**

***Breeding activities and social organization*.** **In south-central New York, breeding takes place in late winter or early spring, usually in lakes, ponds, and swamps (Hurlbert, 1970). Ovulation and egg deposition occur over an extended period (McLaughlin and Humphries, 1978). Females overwintering on land can store sperm for at least 10 months (Massey, 1990). Spawning underwater, the female deposits eggs singly on leaves of submerged plants, hiding and wrapping each in vegetation (Gibbons and Semlitsch, 1991; Smith 1956). The time to hatching depends on temperature (DeGraaf and Rudis, 1983). Smith (1961) found typical incubation periods to be 14 to 21 days in Illinois, whereas the incubation period observed by Behler and King (1979) was 21 to 56 days.**

***Growth and metamorphosis*.** **In late summer or early fall, the larvae transform into either aquatic juveniles or terrestrial efts (Behler and King, 1979). Harris (1987) showed**

that low larval density stimulated neoteny in larvae under experimental conditions. Larval growth rates were higher in ponds with low larval densities (Harris, 1987; Morin et al., 1983). Growth rates for aquatic juveniles are highest in the spring; however, maximum seasonal growth for the terrestrial efts occurs between June and September when the temperature is optimal for active foraging (Healy, 1973).

***Home range and resources*.** For adult newts, Bellis (1968) found the mean distance between capture and recapture sites to be about 7 m, indicating small home ranges. Harris (1981, cited in DeGraaf and Rudis, 1983) did not find any defined home range or any territoriality for males. Most efts around a pond in Pennsylvania remained within 1.5 m of the shore (Bellis, 1968). Healy (1975) estimated the home range for terrestrial efts in a Massachusetts woodland to be 270 m^2 and located approximately 800 m from the ponds where the adults and larvae were located.

***Population density*.** Populations of aquatic adults may reach high local densities, whereas terrestrial efts exhibit lower population densities. Recorded population densities for terrestrial efts range from 34 per hectare (ranging from 20 to 50 efts per hectare) in a North Carolina mixed deciduous forest (Shure et al., 1989) to 300 per hectare in a Massachusetts woodland (Healy, 1975). Harris et al. (1988) observed a density of 1.4 adult newts per m^2 (14,000 adult newts per hectare) in a shallow pond in North Carolina in the winter, whereas the summer population density was only 0.2 adults per m^2 (2,000 adults per hectare).

***Population dynamics*.** Many populations of the eastern newt reach sexual maturity when the eft stage returns to the water and changes to the adult form (Healy, 1974). However, under certain conditions such as low larval density, most of the larvae present have been shown to metamorphose directly into adults or even into sexually mature larvae (Harris, 1987). In experimental ponds, densities of 22 larvae per m^2 resulted in metamorphosis to eft by the majority, while a density of 5.5 larvae per m^2 resulted in metamorphosis directly to the adult form or sexual maturation without metamorphosis (Harris, 1987). Adult density also influences reproduction. Morin et al. (1983) found that doubling adult density resulted in a reduction of offspring produced to one-quarter that produced by adults at the lower density (i.e., from 36 offspring per female in tanks containing 1.1 females per m^2 to 9.7 offspring per female in tanks containing 2.2 females per m^2). The adult life expectancy noted by Gill (1978b) was 2.1 breeding seasons for males and 1.7 breeding seasons for females. Amphibian blood leeches (ectoparasites) are likely to be a primary source of mortality for adults; they also prey directly on larvae (Gill, 1978a).

Similar species (from general references)

- **The black-spotted newt (*Notophthalmus meridionalis*) is similar in size (7.5 to 11.0 cm) to the eastern newt. It has large black spots and is found in south Texas in ponds, lagoons, and swamps. There is no eft stage.**

- **The striped newt (*Notophthalmus perstriatus*) is smaller (5.2 to 7.9 cm) than the eastern newt and ranges from southern Georgia to central Florida. It is found in almost any body of shallow, standing water.**

- **The western newts (*Taricha*) are found along the Pacific coast. They do not undergo the eft stage but rather transform into land-dwelling adults that return to the water at breeding time.**

- **Other small salamanders are similar but vary by having slimy skin and conspicuous costal grooves. They differ in life history, however; in the family *Plethudontidae*, all are lungless and breathe through thin, moist skin. Many are completely terrestrial.**

General references

Behler and King (1979); Conant and Collins (1991); DeGraaf and Rudis (1983); Hurlbert (1969); Smith (1961).

Eastern Newt (*Notophthalmus viridescens*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	adult:					
	B	2.24 ± 0.71 SD	1.12 - 3.52	New York	Gillis & Breuer, 1984	
	F prebreed	3.05 ± 0.06 SE		Virginia	Gill, 1979	
	F postbreed	2.49 ± 0.06 SE				
	M prebreed	2.49 ± 0.03 SE				
	M postbreed	2.76 ± 0.03 SE				
	B spring	1.71 ± 0.43 SD		Massachusetts	Pitkin, 1983	
	B summer	2.13 ± 0.44 SD				
	B winter	1.94 ± 0.33 SD				
	B fall	1.63 ± 0.28 SD				
	larvae:					
	12.8 mm SVL	0.04 ± 0.025 SD		South Carolina	Taylor et al., 1988	
	21.9 mm SVL	0.54 ± 0.167 SD				
	eft:					
	B	1.10 ± 0.40 SD	0.42 - 1.82	New York	Gillis & Breuer, 1984	
	B	1.45		New Hampshire (*viridescens*)	Burton, 1977	
	B summer	1.23	0.63 - 2.17	New York	Stefanski et al., 1989	

Eastern Newt (*Notophthalmus viridescens*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Length (mm SVL)	adult:					
	M	35.0	24 - 44	North Carolina (*dorsalis*)	Harris et al., 1988	
	F	35.0	20 - 42			
	B summer	38.9	33 - 48	New York	MacNamara, 1977	
	juvenile:					
	B spring	26.1 ± 0.35 SE	20 - 32	Massachusetts (*viridescens*)	Healy, 1973	
	larvae:					
	B spring	12.3		s Illinois	Brophy, 1980	
	B fall	19.2				
	eft:					
	B (mm total)	50.4 ± 0.5 SE		North Carolina (*dorsalis*)	Harris et al., 1988	
	B spring	20.5		Massachusetts (*viridescens*)	Healy, 1973	
	B summer	32.7	18 - 41	New York	MacNamara, 1977	
Larval Growth Rate (g/d)	high density:			North Carolina	Harris, 1987	
	-> efts	0.00310		high density: 55,000/ha		
	-> adults	0.00421				
	-> neonates	0.00536				
						1
	low density:					
	-> efts	0.00635		low density: 220/ha		
	-> adults	0.00685				
	-> neonates	0.00676				1
Metabolic Rate (lO_2/kg-d)	efts at 15°C:			New York	Stefanski et al., 1989	
	resting	1.47				
	active	4.27				

Eastern Newt (*Notophthalmus viridescens*)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Metabolic Rate (kcal/kg-d)	basal: A M postbreed A F postbreed larvae (12.8 mm) eft (71.0 mm)	 16.2 16.7 43.5 20.1			 estimated estimated estimated	 2a 2b 2c
Food Ingestion Rate (g/g-d)						3
Surface Area (cm^2)	A M A F	17 15			estimated	4

Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat (measure)	Reference	Note No.
aquatic adults:					New Hampshire (*viridescens*)/small oligotrophic lake	Burton, 1977	
Ephemeroptera		7.5	7.5				
Odonata		31.9	1.9				
Lepidoptera		13.7	0.9				
Diptera		5.8	0.3		(% wet weight; stomach and gut contents)		
other insects		9.9	0.6				
Cladocerans		5.1	84.1				
Amphipoda		5.6	3.1				
Pelycepoda		6.2	1.5				
N. viridescens larvae		11.4	0.0				
other		3.2	0.1				

Eastern Newt (*Notophthalmus viridescens*)

Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat (measure)	Reference	Note No.
efts:					New York/leaf litter surface in forest (% dry weight; stomach contents)	MacNamara, 1977	
Basommatophora		5.5					
Stylommatophora		18.3					
Acari		13.8					
Collembola		10.4					
Thysanoptera		3.4					
Homoptera		4.7					
Coleoptera adult		2.3					
Coleoptera larvae		3.5					
Lepidoptera larvae		7.9					
Diptera adult		9.7					
Diptera larvae		10.6					
Hymenoptera adult		5.8					
larvae:					New Hampshire (*viridescens*)/small oligotrophic lake (% wet weight; stomach and gut contents)	Burton, 1977	
Zygoptera (Odonata)		0.8					
Chironomidae (Diptera)		16.2					
Cladocera		12.7					
Ostracoda		5.3					
Hyallela azteca (Amphipoda)		55.1					
Sphaerium sp. (Pelycepoda)		9.4					
Planorbidae (Gastropoda)		0.5					
Rhizopoda (Protozoa)		0.01					

Eastern Newt (*Notophthalmus viridescens*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/ Habitat	Reference	Note No.
Home Range Size	eft: B	0.0087 ha	0.0028 - 0.0153	Massachusetts (*viridescens*)/ oak/pine forest	Healy, 1975	
	adult: summer	6.86 m		Pennsylvania (*viridescens*)/pond	Bellis, 1968	5
Population Density (N/ha)	A B entire lake A B fringe only	130 - 173 50 - 2,600		New Hampshire (*viridescens*)/small oligotrophic lake	Burton, 1977	
	A winter A summer	50,000 ± 9,000 SE 3,000 ± 1,000 SE		North Carolina (*dorsalis*)/ shallow pond	Harris et al., 1988	
	eft spring	300		Massachusetts (*viridescens*)/ oak/pine forest	Healy, 1975	
	eft summer	34	20 - 50	North Carolina (*viridescens*)/mixed deciduous forest	Shure et al., 1989	
	larvae spring	21,000	0 - 350,000	South Carolina/pond, wetland	Taylor et al., 1988	
	larvae spring summer fall	65,000 ± 15,000 SE 25,000 ± 5,000 SE 10,000 ± 3,000 SE		North Carolina (*dorsalis*)/ shallow pond	Harris et al., 1988	
Clutch Size (eggs)		200 - 400		NS/NS	Behler & King, 1979	
Days to Hatching		14 - 21		Illinois/NS	Smith, 1961	
		21 - 56		NS/NS	Behler & King, 1979	

Eastern Newt (*Notophthalmus viridescens*)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)/ Habitat	Reference	Note No.
Age at Metamorphosis	larvae -> eft	2 - 3 mo		Illinois (*louisianensis*)/NS	Smith, 1961	
		6 mo		Massachusetts (*viridescens*)/inland ponds	Healy, 1974	
	eft -> adult	1 - 3 yrs		South Carolina/ponds	Gibbons & Semlitsch, 1991	
Age at Sexual Maturity	3 - 7 years eft	5 - 6 yrs	4 - 8	Massachusetts (*viridescens*)/inland ponds	Healy, 1974	
	no eft stage	2 yrs		coastal ponds		
Annual Mortality Rates (%)	A F A M	54.1 - 59.5 45.8 - 53.1		Virginia/mountain ponds	Gill, 1978a	
Longevity (breeding seasons)	A F A M	1.7 2.1		Virginia/mountain ponds	Gill, 1978b	

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating/Laying	February - March		April - May	South Carolina	Gibbons & Semlitsch, 1991	
	April		June	North Carolina	Harris et al., 1988	
Hatching	June			Virginia	Gill, 1978a	
	late April			North Carolina	Harris et al., 1988	
		spring		NS	Behler and King, 1979	

Eastern Newt (*Notophthalmus viridescens*)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Metamorphosis to eft	June		September	South Carolina	Gibbons & Semlitsch, 1991	
	mid-August		late November	Virginia	Gill, 1978a	
	mid-July	August - Sept.	early November	New York	Hurlbert, 1970	
Fall Migration (of adults to hibernaculae)	August - Sept.		November	Virginia	Gill, 1978a	
Spring Migration (of adults to breeding ponds)	late March		late April	Virginia	Massey, 1990	

1 "Neonates" refers to newts that become sexually mature in the larval form (i.e., neoteny).
2 Estimated assuming temperature of $20^{\circ}C$ using Equation 3-50 (Robinson et al., 1983) and postbreeding body weights from (a) Gill (1979); (b) Taylor et al. (1988); and (c) Gillis and Breuer (1984). The values for the larvae should be used with caution because these animals are smaller than any used to develop the allometric equations.
3 See Chapters 3 and 4 for methods of estimating food ingestion rates from metabolic rate and diet.
4 Estimated using Equation 3-26 (Whitford and Hutchinson, 1967) and postbreeding body weights from Gill, 1979.
5 Mean distance between capture and recapture sites, suggesting small home range size.

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